#### Peratherium nr. P. fugax (COPE)

Referred specimen.—Vista member: Univ. Colorado Mus. No. 19877; right jaw with M<sub>3</sub>-M<sub>4</sub>; sec. 8, T. 11 N., R. 53 W., Logan County.

This specimen differs in some respects from the Orellan specimens of *Peratherium fugax*. The paraconid of  $M_a$  is high on the trigonid, and the hypoconulid is reduced. Both the paraconid and metaconid appear larger than in *P. fugax*, but this condition may be in part illusionary because of the subequal height of the protoconid and metaconid. Wear may account for the sizes of the cusps. The  $M_4$ , although damaged, shows the same differences in the trigonid, but has a lower paraconid and metaconid. The cingula are weak as in *P. fugax*. In size the specimen resembles *P. fugax*, having an  $M_3$ - $M_4$  length of more than 3.4 mm. (the heel of  $M_4$  is damaged) and a mandibular depth of 3.5 mm. at  $M_3$ .

The specimen is smaller than the type of *P. merriami* Stock & Furlong from the John Day formation of eastern Oregon, and does not have the cingula so well developed. No comparison with *P. youngi* McGrew, of the Miocene of Nebraska is possible, and it remains to be learned whether or not No. 19877 has reached the phylogenetic stage represented by that species.

# Peratherium huntii (COPE)

Herpetotherium huntii Cope, 1873c, p. 5. Peratherium huntii, Cope, 1884a, p. 796.

Cotypes. — AMNH Nos. 5257 and 5275; Brule, Cedar Creek, Colorado (fide Scott, 1941).

Referred specimens.—Cedar Creek member (lower and middle): No. 8159; fragment of left jaw with M<sub>3</sub>-M<sub>4</sub>. No. 8163; fragment of left jaw with M<sub>2</sub>-M<sub>4</sub>. No. 8164; fragment of left jaw with P<sub>4</sub>-M<sub>1</sub>. No. 8315; fragment of right jaw with M<sub>2</sub>-M<sub>4</sub>. No. 8978; right jaw with M<sub>1</sub>-M<sub>4</sub>. All from sec. 7, T. 11 N., R. 53 W., Logan County. No. 8316; fragment of left jaw with M<sub>2</sub>-M<sub>4</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County.

With the exception of No. 8978, these specimens agree closely with the description of the type. Peratherium huntii may be readily recognized and

differentiated from *P. fugax* by much smaller size. In addition it differs from *P. fugax* in having the premolar series uninterrupted and the entoconids of the molars sharper and higher.

No. 8978 differs from other specimens of *Peratherium huntii* in being smaller and having the hypoconulid weaker and more centrally placed on the first three molars. The hypoconulid is not present on M<sub>4</sub>. In this specimen enough of the jaw is preserved to show that the angle of the jaw is inflected as in the Recent opposums.

Peratherium is not at all rare in northeastern Colorado, and McGrew (1939, p. 397) considered it to be abundant in the White River beds of Nebraska. However, I cannot find any record of anyone ever reporting the upper teeth of Peratherium huntii, although the upper teeth of P. fugax have often been reported. In the light of this fact, it seems even more unusual that only upper teeth of Nanodelphys minutus have been found. These facts, together with agreement in size of teeth of P. huntii and Nanodelphys minutus, suggest that P. huntii belongs in the genus Nanodelphys.

#### Nanodelphys minutus McGrew

Nanodelphys minutus McGrew, 1937, p. 452.

Referred specimen.—Cedar Creek member (lower): No. 8997; fragment of maxillary with left M³-M⁴; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County.

With the exception of a smaller stylar cusp A on M³ and a larger stylar cusp E on M⁴, this specimen agrees in detail with the type and a referred specimen, Chicago Natural History Museum No. P25719. A small cuspule on the posterior border of M⁴ between the protocone and metacone, which is not present on the type and the referred specimen, is probably an individual variation. The stylar cusp A on M⁴ seems to be damaged by weathering, but it too probably is smaller than in the type. This damage to M⁴ may account, in part, for the short transverse diameter of the tooth.

With the permission of Dr. McGrew a second set of measurements (Table 1) is given for the specimens described by him (1939).

Table 1.—Measurements (in mm.) of Nanodelphys minutus\*

	No. 8997	No. P25708	No. P25709	No. P25719	No. P25720
M¹, antero-posterior length M¹, transverse width	383 687	(\$0.85±(\$0)	12345	.808.1808.1	1.41
	19.76 - 67.67	1.00	1 477	1 50	1.23
M <sup>2</sup> , antero-posterior length M <sup>2</sup> , transverse width	900 600	1.38 1.53	1.47 1.95	1.50 1.62	1.50 1.50
M <sup>3</sup> , antero-posterior length	1.32	1.17	1.55	1.35	1.00
M <sup>8</sup> , transverse width	1.74	1.59	2022	1.80	
M <sup>4</sup> , antero-posterior length	0.84	444	V 40 4 10	0.75	
M <sup>4</sup> , transverse width	1.70 <sup>b</sup>	2.73.5	* * * *	1.83	F-17-17-12

a. These measurements were made with a binocular grid and checked with calipers. A transverse line through the tip of the protocone and tip of stylar cusp B was used as a base, and all measurements are parallel to or perpendicular to this line.

b. PDamaged.

The possibility that *Peratherium huntii* belongs to this genus has already been considered. The eventual discovery of associated upper and lower teeth will undoubtedly settle the matter, and there is nothing to be gained by a premature reassignment of the species.

#### ORDER INSECTIVORA BOWDICH, 1821

Recent studies of the Oligocene insectivores of northeastern Colorado have materially increased our knowledge of them from this area. Cope (1873b, 1884a) reported three genera, Ictops (as Mesodectes), Domnina, and Geolabis. Matthew (1901) gave no indication that anything other than Proscalops miocaenus was found by the early American Museum expeditions. Patterson & McGrew (1937) added one new genus, Ankylodon, a new species of Metacodon, and confirmed the validity of the genus Domnina. In the present paper I attempt to establish the stratigraphic levels and the associated faunas for most of the genera in a detail not previously known, and, although a matter of lesser importance, new species are named.

# FAMILY SOLENODONTIDAE DOBSON, 1882

# Apternodus iliffensis, new species

Figures 11-12

Holotype.—Part of left maxillary with P³-M³ in occlusion with left lower jaw with P₄-M₃, No. 9112, Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist.

Geological age and locality.—Silt of Chadronian age in the Horsetail Creek member of the White River formation, W% sec. 9, T. 10 N., R. 51 W. (six miles north of Iliff), Logan County, Colorado.

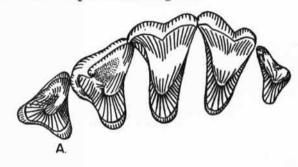
Diagnosis.—Differs from other species of Apternodus in relatively wider P<sup>3</sup>-M<sup>1</sup>, and narrower M<sup>3</sup>; cingula not developed into protocones and hypocones; lower teeth relatively longer with large talonids, especially the talonid of M<sub>3</sub>.

Description.—The small part preserved of the maxillary bone shows that this element resembles the maxillary of Apternodus brevirostris Schlaikjer much more than the corresponding bone in A. gregoryi Schlaikjer. The depression on the maxillary, antero-dorsally to the orbit, does not extend forward beyond M¹. The posterior opening of the infraorbital canal is above the posterior root of M³.

The length of P<sup>3</sup>-M<sup>3</sup> is less than in Apternodus brevirostris or A. gregoryi, and only in the length of P<sup>3</sup> and width of M<sup>1</sup> does this specimen exceed any corresponding dimension of these two species. All the teeth preserved are three-rooted.

The crown of P<sup>3</sup> consists of a central conical cusp, the amphicone, completely encircled by a cingulum that may be best described as weakly developed except on the external surface where it forms a metastyle and a small parastyle. The metastyle is not nearly so high as the amphicone and is united to it by a well-developed crest. This tooth differs from the P<sup>3</sup> of both Apternodus brevirostris and

A. gregoryi in the development of a parastyle and the lack of development of cusps on the anterior and internal parts of the cingulum.



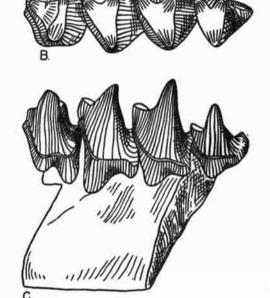


Figure 11.—Apternodus iliffensis, n. sp. No. 9112. (A) Occlusal view of left  $P^3$ - $M^3$ . (B) Occlusal view of left  $P_4$ - $M_3$ . (C) External view of left jaw fragment and teeth. Approximately  $\times$  8.

Basically, P<sup>4</sup> is similar to P<sup>3</sup> in structure, but is more molariform in pattern. The amphicone is higher and is completely surrounded by a cingulum, which is weakest at the lateral border of the posterior surface of the tooth. The internal part of the cingulum is weak, and it is hardly justifiable to say that a cusp is present—certainly not in the sense that cusps are developed in the other species. The antero-external part of the cingulum is developed across the lateral part of the anterior surface of the tooth as a broad, troughlike shelf or upturned wing. The metastyle is well developed and is as high as the amphicone. The large parastyle is located on the external cingulum lateral to the amphicone,

from which, despite wear, it is separated by a valley. The amphicone is similar to those of the molars, and it is only the somewhat triangular shape of the premolar that distinguishes the medial half of P<sup>4</sup>

from the corresponding part of M1.

M¹ has the cingulum complete from the parastyle around the inner border of the tooth to the metastyle. At the internal border, the cingulum is even less expanded than on P⁴, and on the medial part of the anterior face of the tooth the cingulum is reduced to a faint ridge. Antero-externally the cingulum is developed into a winglike, flaring trough similar to that on P⁴ but longer, and is confluent with the parastyle externally. The metastyle is well developed and is extended laterally.

M<sup>2</sup> has a cingulum like that of M<sup>1</sup> but with the winglike trough on the anterior surface weaker, and with the internal part of the cingulum weaker still than on M<sup>1</sup>. The metastyle is relatively much smaller than in the other known species.

M<sup>3</sup> is unusual in this species in its reduction in width relative to the other teeth, virtual absence of a distinct metastyle, and vestigial condition of the

cingulum.

Only the part of the lower jaw containing P<sub>4</sub>-M<sub>3</sub> is preserved, and this fragment indicates that Apternodus iliffensis had a jaw near the size of that of A. mediaevus Matthew and smaller than in either A. brevirostris or A. gregoryi. The preserved teeth show essentially the same pattern as the lower teeth of other species of this genus. A weak cingulum encircles all but the internal surface of each tooth. A well-developed heel, which becomes progressively larger in each succeeding tooth, is present on P<sub>4</sub>-M<sub>3</sub>

Table 2.—Measurements (in mm.) of Apternodus iliffensis

	No. 9112
Crown length of P <sup>3</sup> -M <sup>3</sup>	9.45
Crown length of M1-M3	5.35
P <sup>3</sup> , greatest length P <sup>3</sup> , width at center of crown at alveolus	3.01
P8, width at center of crown at alveolus	2.10
P <sup>4</sup> , greatest length P <sup>4</sup> , width at center of crown at alveolus	2.6
P4, width at center of crown at alveolus	2.9
M <sup>1</sup> , greatest length	2.4
M1, width at center of crown at alveolus	3.9
M2 greatest length	1.81
M <sup>2</sup> , greatest length	3.35
M3 greatest langth	0.00
M <sup>3</sup> , greatest length M <sup>3</sup> , width at center of crown at alveolus	0.99
Crown landt of D. M. at alveolus	2.04
Crown length of P <sub>4</sub> -M <sub>3</sub> at alveolus	7.4
Greatest crown length of P4-M3	7.8
Crown length of M <sub>1</sub> -M <sub>3</sub> at alveolus	5.3*
Greatest crown length of M <sub>1</sub> -M <sub>3</sub>	6.0
Crown length of M <sub>2</sub> -M <sub>3</sub> at alveolus	3.6*
Greatest crown length of M2-M2	4.2
Depth of law on internal side	4 15
P4. greatest length	2.05
r4, greatest width	1.61
M <sub>1</sub> , greatest length	2.19
M <sub>1</sub> , greatest width	1.95
M2, greatest length	2.14
M <sub>2</sub> , greatest width	
M <sub>3</sub> , greatest length	2.21
M <sub>8</sub> , greatest width	1.40
many Browness middle strategic strat	1.40

a. Estimated.

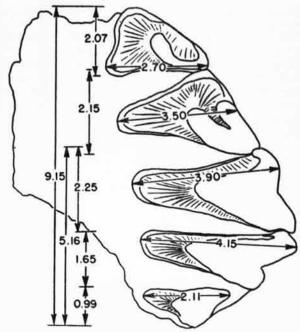


FIGURE 12.—Apternodus iliffensis, n. sp. No. 9112. Dimensions of left P<sup>8</sup>-M<sup>8</sup> in millimeters. All anteroposterior measurements are parallel to antero-posterior axis of the skull. All transverse measurements are made with occlusal surfaces oriented to agree with their natural position in the skull.

and results in M<sub>s</sub> having a heel larger than in any of the other known species. The paraconids are not so well developed, and the teeth are more slender and higher crowned than in the other species. P<sub>4</sub> has progressed toward a molariform pattern to the extent that only the more closely set cusps, more narrow width, and slightly shorter crown distinguish it from M<sub>1</sub>. The trigonid of P<sub>4</sub> forms an equilateral triangle, but in all the molars, the trigonids are a little wider transversely.

Two sets of measurements are given for this species. One set (Table 2) was made following the methods of Schlaikjer (1933, 1934), which were not entirely satisfactory for this particular specimen. The second set of measurements was made in ac-

cordance with the diagram in Figure 12.

Discussion.—Compared to Apternodus brevirostris the teeth of this species have a greater stylar development and molarization of the premolars, progressive simplification and reduction of size in the last two molars, and less development of internal cingular cusps on all the teeth. The lower teeth retain the relatively narrow trigonids, but have relatively enlarged talonids, and show molarization of the premolars. With A. mediaevus, which is represented by two lower molars, as a means of comparison, the reduction of the cingula on the lower teeth is seen as a character common to the other species.

The dominant teeth in the upper and lower dental arcades are the first molars as in A. brevirostris and A. gregoryi; yet, with the exception of the lower

premolars of A. gregoryi, molarization appears to

have advanced more in A. iliffensis.

The dentition of A. iliffensis is smaller than that of A. brevirostris and A. gregoryi, but may have been larger than that of A. mediaevus. Relatively, however, P<sup>4</sup> is shorter, M<sup>1</sup> wider, and M<sup>3</sup> much narrower. These relationships bear out the observation that the upper teeth of this species had greater molarization of the premolars and reduction of the last two molars.

It is noteworthy that the reduction of the M<sup>3</sup> is in width and that, although it is a weak and reduced tooth, relatively and actually, it still retains the length necessary to occlude with the elongate and well-developed heel of the lower third molar.

The heel of M<sub>3</sub> is actually large, but, like that of A. gregoryi, and in contrast to that of A. mediaevus, there has been a reduction of the trigonid (more so than in A. brevirostris) that emphasizes the size of

the structure.

Development of the cingula is characteristic of these three specimens: there are incomplete cingula on the upper teeth of A. brevirostris, which are, nevertheless, well developed internally; there are complete and well-developed cingula on the teeth of A. gregoryi; and there are complete cingula on the teeth of A. iliffensis, which are not well developed internally, although the premolar parastyles seem to be more advanced than in other species.

With only four recorded specimens from four different localities (and described as four different species), it is difficult to distinguish individual variations from trends in evolution. Despite the absence of the upper teeth of A. mediaevus, this new species is considered to be structurally advanced beyond A. mediaevus and to be deviating

from A. brevirostris.

## FAMILY LEPTICTIDAE GILL, 1872

#### Ictops nr. I. bullatus MATTHEW

Referred specimen.—Cedar Creek member (middle): No. 8151; skull and lower jaws with fragments of the skeleton; SE¼ sec. 7, T. 11 N., R. 53 W., Logan County.

This specimen is tentatively placed near the species *I. bullatus* Matthew, and the salient characters—that is, those characters emphasized by previous workers such as Cope, Leidy, and Matthew, and summarized by Scott (Scott & Jepsen, 1936)—are as follows:

(1) Temporal ridges sinuous; thus like Ictops and

unlike Leptictus.

(2) Skull broad for length, being proportionately wider than that of Leptictus haydeni Leidy (which is wider than any species of Ictops). Otherwise the proportions are similar to those of Leptictus.

(3) Size large; thus like both Ictops bullatus and

Leptictus haydeni.

(4) Muzzle narrow, and has some medial offset, as in Leptictus. (5) P³ with internal and postero-external cusps; thus like *Ictops* and unlike *Leptictus*. In addition this tooth (and P⁴-M¹) has a welldeveloped antero-external cingular cusp.

(6) P¹-P² with some medial offset, and P³ rotated with anterior end directed antero-medially, conforming with the medial offset of the

muzzle.

(7) M<sub>3</sub> reduced, more so than in any species of Ictors.

(8) P¹-P² have posterior accessory cusps, which other species do not have.

(9) P4-M1 have relatively narrow transverse di-

ameters.

(10) P<sub>1</sub> double rooted. Scott (Scott & Jepsen, 1936, p. 14) states that P<sub>1</sub> of *Ictops* is single rooted.

Among the characters that serve to distinguish Leptictus are absence of an internal cusp on P³, offset of the muzzle at P³, and alignment of the outer side of the premolar tooth row with the inner side of the molar tooth row. In Ictops the internal cusp is present, and there is no offset to the muzzle or break in the dental arcade at the end of P³. However, Cope described a genus and species (Isacus caniculus, 1873b, p. 3; Mesodectes caniculus, 1875, p. 30; now considered to be in the genus Ictops) based on one specimen from northeastern Colorado, that differed from Ictops only in having the postero-external cusp absent on P³. The postero-external cusp is absent in Leptictus but seems to be normally present in Ictops.

No. 8151 approaches Leptictus in some ways but has more characters in common with Ictops. Characters similar to those of skull No. 8151 are present in a leptictid skull, No. 2568, from Custer County, South Dakota, which possibly was the one referred to by Matthew (1937, p. 217) as an "undescribed species of Leptictus." Although having sinuous temporal crests, internal cusps present on P³, postero-external cusps reduced or absent on P³, and P¹-P² in line with the internal margins of the molars, the skull from South Dakota has the added distinction of large size, being 73 mm. long as measured without part of the muzzle, the addition of which would make it at least 75 mm. long. This is about 10 mm. longer than any other leptictid skull known to me. Also, the teeth are unusually wide.

These specimens that have been commented upon show, in addition to other characters, variation in the structure of P<sup>3</sup> ranging from a single cusp to a multiplicity of cusps. It would appear that the structure of P<sup>3</sup> is linked with the sharpness of the break or offset of the muzzle and the premolar alignment, and hence to the ratio of the length and breadth of the muzzle compared with the rest of the skull. No. 8151, however, differs from the usual condition in having the slightly offset muzzle and premolars combined with a strong tendency to form accessory cusps on the premolar. Individual

variation and differences between the species are such that it is possible to conceive of a series of independent genetic factors that control each of the areas and parts of the skull in varying degrees of intensity, thus giving rise to variations which do not correlate with each other. If there is no great degree of variability in leptictid skulls, then specimens No. 2568 and No. 8151 probably represent new species. But, with the number of species of Oligocene leptictids known at present, it would be premature to name the specimens before the Oligocene genera have been revised.

#### Ictops sp.

Specimens of leptictids consisting of fragments of upper and lower jaws have been collected by me from exposures of the Cedar Creek member in secs. 7 and 28 of T. 11 N., R. 53 W., and sec. 12, T. 11 N., R. 54 W. in Logan County. All have been referred to the genus *Ictops*, and most of the material is probably of the same species as No. 8151, discussed above. Although variation in size is considerable among these fragments, especially in depth of lower jaw and width of teeth, one lower jaw fragment, No. 8149, may represent a second, slightly smaller species that coexisted with the larger form—a species with narrower cheek teeth and shallower jaws, perhaps *Ictops dakotensis*.

# FAMILY ERINACEIDAE BONAPARTE, 1838 Metacodon magnus Clark

Metacodon magnus Clark (in Scott & Jepson, 1936, p. 22).

Referred specimen.—Cedar Creek member (lower): No. 8155; right ramus with M<sub>1</sub>-M<sub>3</sub>; SW¼ sec. 21, T. 11 N., R. 53 W., Logan County.

If the material referred to this species is correctly assigned, it extends the range of the species from the Chadronian into the Orellan.

#### Metacodon mellingeri Patterson & McGrew

Metacodon mellingeri Patterson & McGrew, 1937, p. 258.

Type.—Chicago Nat. Hist. Mus. No. P15321; Cedar Creek member, sec. 17,20 T. 11 N., R. 65 W., Weld County, Colorado.

Referred specimens.—Cedar Creek member (lower and middle): Nos. 8156-8157; right lower jaw fragments, each with one molar; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County. No. 8158; right M<sub>3</sub>; E½ sec. 7, T. 11 N., R. 53 W., Logan County. No. 8161; right jaw with P<sub>3</sub>-M<sub>3</sub>; SE¼ sec. 7, T. 11 N., R. 53 W., Logan County.

Patterson & McGrew described this species in detail. My study of the material from Logan County reveals nothing significant to add to their discussion.

CLARK (in Scott & Jepsen, 1936, p. 22; Clark, 1937, p. 310) placed the genus *Metacodon* in the family Leptictidae, and Patterson & McGrew (1937, p. 257) placed the genus in the Erinaceidae. Later Clark (1939, p. 139) commented upon the observations of Patterson & McGrew but did not believe that the evidence warranted a definite as-

signment one way or another. BUTLER (1948, p. 491) created a new family, the Metacodontidae, to receive this and other genera stating: "This new family is created to include the genera Metacodon, Meterix, and Plesiosorex which, although they may eventually prove to be related to the Erinaceidae, are too imperfectly known to be placed with certainty in that family." I have no intention of passing upon the merits of the arguments offered by CLARK OF PATTERSON & McGrew for placing the genus Metacodon in either of the two families. Regardless of Butler's evidence of the homogeneity of this group of genera that make up his family Metacodontidae, his argument that the genera are too imperfectly known to be included in the Erinaceidae would seem to apply equally well to the thesis that they are not well enough known to warrant creating a new family. I leave the genus in the Erinaceidae because the family is a convenient taxonomic unit in which to place this Oligocene genus of uncertain systematic position.

# Ankylodon annectens Patterson & McGrew

Ankylodon annectens Patterson & McGrew, 1937, p. 269.

Type.—Chicago Nat. Hist. Mus. No. P15326; Cedar Creek member, sec. 17, T. 11 N., R. 65 W., Weld County, Colorado.

The species is only known from the type locality.

# Ankylodon progressus, new species

Figure 13

Holotype.—Posterior part of a right ramus with M<sub>1</sub>-M<sub>3</sub>, No. 8153, Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist. Geological age and locality.—Silts of Orellan age in the Cedar Creek member (lower) of the White River formation, Clyde Ward Ranch, SW½ sec. 12, T. 11 N., R. 54 W., Logan County, Colorado. A referred specimen, No. 8152, a left jaw with M<sub>1</sub>-M<sub>3</sub> was found in the Cedar Creek member (middle) in SW½ sec. 21, T. 11 N., R. 53 W., Logan County.

Diagnosis.—In comparison with the type species (Ankylodon annectens Patterson & McGrew, 1937) the first two molars of this species have the hypoconulids reduced; the principal cusps in transverse alignment instead of oblique, and with the protoconids equal in height to the metaconids instead of higher; and the anterior cingula less developed. Compared with referred specimens of A. annectens, the heel of the M<sub>3</sub> is narrower in this new species.

Description.—This species does not differ from Ankylodon annectens in the known parts except in larger size (Table 3) and the details given in the diagnosis. Concerning the specific differences, it is to be noted that on M<sub>1</sub> and M<sub>2</sub> the hypoconulid is represented only by a slight, posteriorly directed bulge on the rear of the tooth. These two molars have the principal cusps in transverse alignment, a condition resembling that seen in the species of Metacodon Clark, but decidedly different from that in A. annectens which has the metaconids and entoconids in advance of their neighboring cusps.

<sup>20.</sup> The locality reference of the type specimen by PATTERSON & McGrew to sec. 12 was an error.

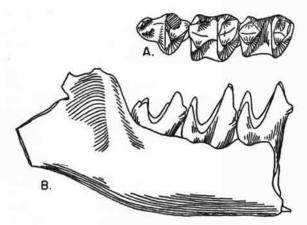


FIGURE 13.—Ankylodon progressus, n. sp. No. 8153. (A) Occlusal view of right  $M_1$ - $M_3$ . (B) External view of right jaw with teeth. Approximately  $\times$  7.

In A. progressus the metaconids have larger bases than the protoconids but are equal to the protoconids in height. The entoconids are much higher than the hypoconids and have larger bases as in A. annectens, but relatively the entoconids of A. progressus are much higher than those on the molars of A. annectens. A cingulum is present on the antero-external surface of M<sub>1</sub> and M<sub>2</sub> below the paraconid ridge. This cingulum is a short ridge (0.5 mm. and 1.0 mm. long on M<sub>1</sub> and M<sub>2</sub>, respectively) directed diagonally downwardly and outwardly. These remnants of the cingula represent the last stage before complete loss. Ankylodon annectens had much better developed cingula, yet PATTERSON & McGrew rightly described them as weak. A. progressus has the paraconids reduced to mere ridges as in A. annectens. In the type specimen of A. progressus there is more reduction of the paraconid in M2 than in M1. This may be an individual variation since a damaged referred specimen has the paraconid on M<sub>1</sub> more reduced than that on M2.

In the new species the paraconid of  $M_s$  is reduced to a ridge equal in size to that on  $M_1$ . The metaconid has been broken off, but the base of the cusp is larger than that of the protoconid. The anterior cingulum is less reduced than on  $M_1$  or  $M_2$ . The

entoconid is much higher than the hypoconid, and the hypoconulid is well developed, distinct, and almost as large as the entoconid. The hypoconulid lies postero-internally from the entoconid on the median part of the rim of the heel but is more closely associated with the entoconid than the hypoconid, from which it is separated by a large notch.

Table 3.—Measurements (in mm.) of Ankylodon progressus

	No. 8153
Crown length of M <sub>1</sub> -M <sub>3</sub>	5.91
M <sub>1</sub> , antero-posterior length	1.95
M <sub>1</sub> , transverse width of anterior lophid	
M <sub>1</sub> , transverse width of posterior lophid	
M2, antero-posterior length	
Mo. transverse width of anterior lophid	1.76
M2, transverse width of posterior lophid	1.54
Ma. antero-posterior length	2.16
M <sub>3</sub> , transverse width of anterior lophid	1.35
M <sub>3</sub> , transverse width of posterior lophid	0.90

# FAMILY SORICIDAE GRAY, 1821

#### Domnina gradata Cope

Domnina gradata Cope, 1873b, p. 1.

Type.—AMNH No. 5353; Brule (probably lower), Cedar Creek, Colorado (fide Patterson & McGrew, 1937).

Referred specimens.—Cedar Creek member (lower): No. 8353; left jaw with M<sub>1</sub>-M<sub>3</sub>; SE¼ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8160; left jaw with M<sub>2</sub>-M<sub>3</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County. Chicago Nat. Hist. Mus. No. P15320; left jaw with I<sub>3</sub>, P<sub>4</sub>-M<sub>3</sub>; sec. 17, T. 11 N., R. 65 W., Weld County.

Cedar Creek member (widdle): No. 8977; left jaw with

Cedar Creek member (middle): No. 8977; left jaw with M<sub>1</sub>-M<sub>3</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County.

Patterson & McGrew (1937) discussed this species, including the material from Weld County, and Cope's type. The specimens from Logan County are similar in structure to, and are within the size range of, the type of *D. gradata* and referred specimens from Nebraska and Weld County (Table 4).

#### Domnina compressa, new species

#### Figure 14

Holotype. — Posterior part of right ramus with M<sub>1</sub>-M<sub>3</sub>, No. 8154, Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist. Geological age and locality.—Silts of Orellan age in the Cedar Creek member (middle part) of the White River

Table 4.—Measurements (in mm.) of Domnina gradata\*

	No. 8160	No. 8353	No. 8977	Patterson & McGrew
Crown length of M <sub>1</sub> -M <sub>3</sub>	0747	i roi	5.25	5.4-5.8
M <sub>1</sub> , antero-posterior length			2.07	2.2-2.5
M <sub>1</sub> , transverse width	4 - 1 - 4 - 4 -	(6)4(6)	1.41	1.4-1.5
M <sub>2</sub> , antero-posterior length	2.10	1.98	1.74	1.8 - 2.1
M2, transverse width	1.35	1.41	1.29	1.2-1.4
M <sub>3</sub> , antero-posterior length	1.59	1.50	1.44	1.5-1.8
M <sub>3</sub> , transverse width	1.05	1.05	0.96	1.1-1.2
Depth of ramus at M <sub>1</sub>	WW. W. W.	54 (1956)	2.41	2.2-2.5
Depth of ramus at M2		2,44	2.40	2.5
Depth of ramus at M <sub>3</sub>	2.30	2.25	2.32	

a. The following measurements include, besides those for the specimens found by me, the maximum and minimum measurements given by PATTERSON & McGrew (1937, p. 256) for the specimens examined by them.

formation, SW¼ sec. 21, T. 11 N., R. 53 W., Logan County, Colorado.

Diagnosis.—Differs from Domnina gradata Cope and Domnina thompsoni Simpson in having: tooth row shorter, with the trigonids and talonids compressed antero-posteriorly relative to the width; entoconids separated from the metaconids by a notch; antero-external cingulum weak; and basin of heel of M<sub>3</sub> enlarged, with hypoconid and hypoconid crest better developed and more labial in position.

Description.—The jaw is slightly lighter anteriorly than in Domnina gradata and possibly was shorter, since the angle of the root of the third incisor in the jaw is more acute and the molar tooth row is short. The coronoid ridge is prominent and passes downward onto the side of the ramus as in D. gradata; but the side of the mandible is swollen, and the ridge seems to grade into this expanded part. On the internal surface of the ramus, under the paraconid of M, and close to the inferior border, there is a foramen—possibly a nutrient canal. The mental foramen is below the talonid of M<sub>1</sub>. A feature of the ramus of this specimen is the presence of an elongate depression or pit below P, and the trigonid of M1, anterior to the mental foramen and above the root of the incisor. Specimens of D. gradata from Logan and Weld Counties have only the faintest trace of this depression. The inferior border of the ramus is more convex than in D. gradata. Most of the ascending ramus is missing, but the lower part of the intertemporal fossa is preserved.

Following the suggestion of Patterson & McGrew (1937), the teeth of this specimen were examined under ultraviolet light. Like Cope's holotype there is no evidence of pigmentation in ordinary light, but the teeth fluoresced orange over an area of the teeth corresponding to the pigmented areas on the specimens of *Domnina gradata* examined by Patterson & McGrew.

The molar teeth are smaller (Table 5) than those of *Domnina gradata*, being practically the size of

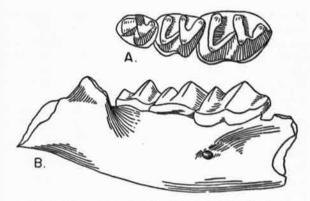


FIGURE 14.—Domnina compressa, n. sp. No. 8154. (A) Occlusal view of right  $M_1$ - $M_3$ . (B) External view of right jaw with teeth. Approximately  $\times$  9.

the molars of *D. thompsoni*, and are crowded together antero-posteriorly more than in either of these two species. Both M<sub>2</sub> and M<sub>3</sub> have the whole of their paraconids lapping over onto the preceding teeth. At a point under P<sub>4</sub>, the incisor is slightly compressed laterally in cross section. The posterior

part of the alveolus of P<sub>4</sub> is preserved.

M, is the largest of the molars and, like the other molars, is swollen laterally. Compared to that of Domnina gradata, the trigonid of D. compressa is short antero-posteriorly but exceeds the size of the talonid. The protoconid rises above the other cusps, which are about equal in height, and it is anterior to the metaconid. The talonid is wider than the trigonid and has the anterior slope of the hypoconid forming a crest or facet of wear, which is directed inward and forward to join the posterior face of the trigonid at the mid-line of the tooth below the protoconid-metaconid crest. A similar transverse facet of wear extends from the hypoconid to the posterior end of the entoconid. There is no evidence of a hypoconulid in the present stage of wear. The entoconid is well developed, not transversely compressed as in D. gradata, and is separated from

Table 5.—Measurements (in mm.) of Domnina compressa, Domnina thompsoni, and Domnina crassigenisa

	Domnina compressa, No. 8154	Domnina thompsoni, AMNH No. 32647	Domnina crassigenis Cope, 1874a Cope, 1		
Crown length of M <sub>1</sub> -M <sub>3</sub>	4.44	4.8	2010:2/22/2010		
Crown length of M <sub>2</sub> -M <sub>3</sub>	4.44		2.2	3.2	
M <sub>1</sub> , antero-posterior length	1.98	1.8			
M <sub>1</sub> , transverse width	1.00		4 5 4 4	* * * *	
A, antere mentales I at	1.38	1.2			
M2, antero-posterior length	1.56	1.5	4.00	14.55	
M <sub>2</sub> , transverse width	1.20	1.1	1111	1.4	
M <sub>3</sub> , antero-posterior length	1.26	1.3	1.8	1.2	
Ma, transverse width	0.90	0.8			
Depth of ramus at M	2.28	2.0(Ca.)	S#5.#3#5#3	10.00	
Depth of ramus at M2	2.40	1/2005 THE RESERVED BY			
South of samue at M	2.40	* * * * *	3.50	3.0	
Depth of ramus at M <sub>3</sub>	2.22	a (a) 4 (a)	3.0	27/4/4	

a. These measurements include, besides those for the type of *Domnina compressa*, the measurements given by Simpson (1941, p. 2) for the type of *D. thompsoni* and two sets of measurements given by Cope (1874a, p. 470; 1884a, p. 811) for the type of *D. crassigenis* which is to be discussed in the following pages. Measurements of *D. compressa* were made by grid and checked by calipers.

the metaconid by a valley. The antero-external cingulum is noticeably weaker than in D. gradata, but extends from the anterior tip of the paraconid to the postero-external corner of the protoconid where it joins the hypoconid cingulum. The hypoconid cingulum extends around the rear of the tooth and passes under the cingulum of  $M_2$ .

M<sub>2</sub> is smaller than M<sub>1</sub> and has a proportionately longer talonid, which, however, does not exceed the trigonid in width. Both the metaconid and entoconid are proportionately better developed than on M<sub>1</sub>, and the protoconid seems to be reduced. Otherwise the relationships of the cusps, crests, and cin-

gula are as on M<sub>1</sub>.

M, is the smallest of the molars. Although the metaconid has been broken, the trigonid appears to be a miniature of those in M1 and M2. The talonid of M3 differs from that of Domnina gradata in being larger, in having the hypoconid more labial in position, and in having the crest from that cusp extending to the mid-line of the posterior face of the trigonid as in the first and second molars. This, together with the compressed entoconid, serves to form a basin in the heel of the tooth which is relatively larger than in D. gradata. Although on M<sub>3</sub> of D. gradata the entoconid is either absent or reduced, in this new species it is present as a high, transversely compressed ridge, which is separated from the metaconid by a notch. In this molar, as in the others, there is a better union of the entoconid to the hypoconid by the posterior ridge of the tooth than is seen in D. gradata. The antero-external cingulum is relatively better developed on Ma than on the other molars and passes around the base of the protoconid to unite with the hypoconid. There is no hypoconid cingulum.

Discussion. — Cope (1873c, p. 8) and Scott (1894, p. 446) described species of soricids which were subsequently placed as synonyms of Domnina gradata, or otherwise disposed of. Although there is no doubt of the correctness of this procedure, it is thought best to review the synonyms to make it clear that none of them will be revived and applied to D. compressa.

Miothen gracile Cope (1873b, p. 8) was transferred by its author to Domnina (1874a, p. 470) and later assigned by him to Peratherium huntii (Cope) (1884a, p. 796). I have not seen the type of this species, but it is evident from Cope's description that it is not D. compressa. Cope's Domnina crassigenis (1874a, p. 470) [Miothen crassigenis (1873b, p. 8)] was placed in the synonymy of D. gradata by Patterson & McGrew (1937, p. 248). They stated: "The holotype of D. crassigenis (Cope) consists of a pair of incomplete mandibles with heavily worn lower molars. The specimen shows no characters that might serve to separate it from D. gradata." Cope (1874a, p. 470) pointed out that the teeth of D. crassigenis were less robust than in D. gradata; described the third molar as re-

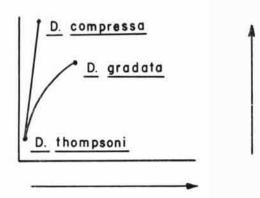
duced, diamond-shaped and longitudinal, and onehalf the size of M2; and gave dimensions (Table 5). Ten years later Cope (1884a, p. 811) emphasized the equal size of the trigonid and talonid of M2, and the small size of M<sub>s</sub>, it being equal in size to the talonid of M2. A second set of measurements was given. These descriptions do not fit D. compressa, and the only measurement that needs serious consideration is the length of M3 given in 1884. Concerning this, it is of significance that both Cope and Patterson & McGrew stressed the great amount of wear on the type. Extreme wear on Ma of D. gradata would produce the length given by COPE in 1884 and the description, by comparison to M2, of the M<sub>3</sub> size given in the text (1884a, p. 811). Protosorex crassus was described by Scott in 1894 (p. 446) and placed in the synonymy of D. gradata by Patterson & McGrew (1937, p. 248). They state that "The description and measurements given by Scott for *P. crassus* indicate that this species must be placed in the synonymy of *D. gradata*." There is nothing in Scott's description or measurements that definitely separates Protosorex crassus from D. compressa or, for that matter, from several soricids. On the other hand, nothing in Scott's description demonstrates that the P. crassus specimen is more likely to be D. compressa than D. gradata. Since the unfigured type is lost, however, and the description is essentially generic, there can be no better solution than to consider Protosorex crassus a synonym of D. gradata. The fact that the type of P. crassus came from South Dakota reduces the chance of its being D. compressa.

Domnina gradata and D. compressa seem to represent two divergent branches that could have developed from D. thompsoni of the Chadron. Assuming this to be true, the trend suggested by D. compressa was toward the loss of the crest uniting the entoconid and metaconid, retention of a broad heel on M<sub>3</sub> with movement of the hypoconid and hypoconid crest in a labial direction, more rapid or better union of the entoconid with the hypoconid, and greater reduction of the jaw. The trend suggested by D. gradata was toward reduction of the heel of M<sub>3</sub> (relative to total size of the tooth), slower loss of the union of the entoconid with the metaconid, slower union of the entoconid with the hypoconid, and less reduction of the jaw. These apparent trends are shown diagrammatically

in Figure 15.

Morphologically, *Domnina compressa* seems closer to the modern soricids than is *D. gradata*, and no characters are to be found that would bar it from a position as structural ancestor to the Recent soricids with pigmented teeth.

In the three species mentioned above, the loss of the hypoconulid as a distinguishable entity probably occurred early in their phylogenetic history perhaps sometime in the Eocene.



- I. Degree of M3 reduction
- 2. Degree of size increase.

- I. Degree of jaw reduction.
- Degree of entoconid isolation from metaconid.
- Degree of entoconid and hypoconid union.

Position of the three species indicates trend, and not units of degree other than greater or lesser.

FIGURE 15.—Diagrammatic chart showing trend of changes undergone by *Domnina compressa* and *Domnina gradata* as compared with *Domnina thompsoni*.

#### Family TALPIDAE Murray, 1866

## Proscalops miocaenus MATTHEW

Proscalops miocaenus Matthew, 1901, p. 375.

Type.—AMNH No. 8949a; Leptauchenia beds, White River formation, Colorado.

The type of this species is a skull and jaws, and is the only reported specimen.

On one occasion, the type of *Proscalops secundus* Matthew <sup>21</sup> was referred to under the name *P. miocaenus*, but apparently not with intention to synonymize the names (Gregory, 1910, p. 238, legend for fig. 17, no. 9).

#### Proscalops sp. (Small form)

Referred specimen. — Cedar Creek member (middle): No. 8143; left jaw with P<sub>1</sub>-P<sub>2</sub>, alveolus of P<sub>3</sub>, and P<sub>4</sub>-M<sub>3</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County.

No. 8143 represents an unnamed species of *Proscalops*, smaller than *P. miocaenus* and with a relatively smaller M<sub>1</sub> and smaller talonids on the molars. In the Chicago Natural History Museum there is a skull and jaws from the middle Oligocene of Wyoming that resembles this specimen. Specific assignment of No. 8143 is deferred until the Wyoming specimen is prepared and studied.

#### Scalopine sp.

Referred specimen. — Cedar Creek member (middle): No. 9224; right humerus lacking proximal articular surfaces; SE4 sec. 7, T. 11 N., R. 53 W., Logan County.

This bone is approximately three-fourths the size of the humerus of *Scalopus aquaticus machrinoides*, but otherwise does not differ in any respect from that of the Recent form.

I suggest that this typically talpid humerus is associated with *Proscalops*. While the association cannot be proved, at least it weakens the argument (Schlaßer, 1933, p. 23) for association of *Proscalops* with the humerus of *Arctoryctes*—a bone that certainly is not talpid-like.

#### ?INSECTIVORA, incertae sedis

#### Arctoryctes?

Referred specimens.—Cedar Creek member (middle): Nos. 9837-9838; right humerus with damaged capitulum, and left humerus lacking proximal articular surfaces (not associated); W½ sec. 7, T. 11 N., R. 53 W., Logan County. No. 9839; right humerus lacking the medial border; NE½ sec. 3, T. 11 N., R. 54 W., Logan County.

These humerii are basically similar to the type of Arctoryctes terrenus Matthew. Unlike the humerus of A. terrenus, these specimens have the teres tubercle developed into a distinct process. Together, the teres tubercle and the pectoral process (deltoid process of Schlaikjer, 1933 <sup>22</sup>) convert the bicipital

<sup>21.</sup> Proscalops secundus has never been adequately described. So far as I can ascertain, the type designation and specific name must be cited as figures 3 and 4 of plate 51, and the accompanying legends on page 559 of "The Carnivora and Insectivora of the Bridger Basin Middle Eocene" (MATTHEW, W. D., 1909, Am. Mus. Nat. Hist., Mem., vol. 9, pt. 6). Compared with P. miocacnus the major distinguishing features of the type specimen (AMNH No. 13768) are: Skull longer (28 mm.) and wider; M³ relatively longer (antero-posterior length 1.8 mm., and transverse width 2.14 mm.); paracones, metacones, and protocones of P³-M³ broader and more shelflike; and styles more elongate and sharper antero-posteriorly.

<sup>22.</sup> The identity of this structure may depend upon the systematic position of Arctoryctes. If Arctoryctes is an insectivore, particularly a talpid, the structure may be the proximal end of the pectoral crest which has migrated downward to its present position. On the other hand, the process may be truly homologous to the deltoid process seen in other orders. See, for example, the humerii of Metacheiromys or Galliaetatus.

groove into a deep well-protected channel. These specimens show a fossa similar to the fossa that lies medial to the trochlea on Scalopus.

#### Geolabis rhynchaeus COPE

Geolabis rhynchaeus COPE, 1884a, p. 808.

Type.—AMNH No. 5347; northeastern Colorado.

This genus and species was based on parts of two crania that lacked molars and are yet the only known specimens. Cope (1874a, p. 469) originally thought they might represent members of the genus Domnina and in 1884 regarded the specimens as possibly being talpids. Scott & Jepsen (1936, p. 25) placed the genus in the family Talpidae.

# ORDER LAGOMORPHA BRANDT, 1855 Family LEPORIDAE Gray, 1821

Several hundred leporid specimens were collected in northeastern Colorado, and their occurrence was recorded in five-foot units in the measured section of each exposure or closely related

exposures.

At present the leporids seem to offer a rather convenient stratigraphic index to the Oligocene beds in northeastern Colorado. Whether or not this will continue to be the case depends upon the results of careful collecting and analysis of the leporid fauna of each exposure and level. The Horsetail Creek member carries only Palaeolagus intermedius. In the beds that grade from the Horsetail Creek member into the Cedar Creek member, Palaeolagus haydeni and P. intermedius are found. Following P. haydeni in the section comes Palaeolagus burkei, the smallest rabbit of the genus. It survived throughout the middle and upper parts of the Cedar Creek member and, from the meager evidence present, continued on into Whitneyan time along with P. intermedius.

It may be pointed out here that enough material now is present from each of the various levels and exposures to give a good picture of tooth wear from immaturity to old age of these rabbits. A survey of the lower teeth of Palaeolagus intermedius, P. haydeni, and P. burkei, each species represented by teeth from a separate and single locality, showed that the stages of wear were not comparable in the three groups. For example, the young of P. burkei either shed their deciduous teeth relatively early in life, or else were confined to a habitat that was advantageous to longevity, because few jaws with deciduous teeth were found. Such specific peculiarities may never be explained, but this leporid collection presents many problems for the future student. It is outside the scope of this study to

Green (1942) studied the Oligocene leporids in the collection of the University of Kansas which included specimens from northeastern Colorado. Unfortunately, he did not have either the strati-

graphic control or the quantity of material now present; consequently, no attempt is made to correlate my work with that of GREEN.

# Palaeolagus intermedius MATTHEW

Palaeolagus intermedius MATTHEW, 1899, p. 53.

Type.—AMNH No. 8722, upper levels of the White River, at Castle Rock, Cedar Creek, Colorado.

Referred specimens.—Horsetail Creek member: No. 9011; left P<sub>4</sub>-M<sub>2</sub>; SE¼ sec. 1, T. 10 N., R. 54 W., Logan County. No. 9095; left jaw with P<sub>3</sub>-M<sub>2</sub>; W½ sec. 30, T. 11 N., R. 51 W., Logan County. No. 9109; six lower jaws; W½ sec. 29, E½ sec. 30, T. 11 N., R. 53 W., Logan County. No. 9129; left maxillary with P<sup>4</sup>-M<sup>2</sup>, and four fragments of lower jaws; NE¼ sec. 31, T. 11 N., R. 56 W., Weld County. No. 9132; right maxillary and two left lower jaws; N½ sec. 13, T. 11 N., R. 56 W., Weld County.

Horsetail Creek member or Cedar Creek member (lower): No. 9094; right jaw with P<sub>4</sub>-M<sub>3</sub>; NE¾ sec. 8, T. 11 N., R. 54

No. 9094; right jaw with P<sub>4</sub>-M<sub>3</sub>; NE<sup>4</sup> sec. 8, T. 11 N., R. 54 W., Logan County. No. 9097; associated upper and lower jaws; SE<sup>4</sup> sec. 17, T. 11 N., R. 65 W., Weld County. No. 9098; same as No. 9097. No. 9099; 4 upper and 20 lower jaws; locality same as No. 9097.

Cedar Creek member (middle): No. 9092; damaged skull; SE4 sec. 3, T. 11 N., R. 54 W., Logan County. No. 9093; right maxillary with P<sup>2</sup>-M<sup>2</sup>; center sec. 3, T. 11 N., R. 54 W., Logan County.

The type locality was recorded by MATTHEW (1902b, p. 308) as above. From the evidence in the 1898 field records, I think Castle Rock is in either R. 53 or R. 54, T. 11 N., Logan County.

MATTHEW'S record of *Palaeolagus intermedius* 

from the Leptauchenia zone and the referred specimens in our collections establish the range of this species as throughout the Oligocene in northeastern

Colorado.

The teeth of Palaeolagus intermedius resemble those of P. haydeni more than those of P. burkei. Compared with the teeth of P. haydeni, the upper teeth of P. intermedius are relatively much wider, actually larger, and in the cycle of tooth wear, lose their crescents and hypostria much earlier in life. There is apparently a greater length of time between eruption of successive teeth. In the specimens from the Horsetail Creek member, the length of P3-M2 ranges from 8.0 mm. to 8.9 mm., and the length of P<sub>4</sub>-M<sub>2</sub> ranges from 6.7 mm. to 7.6 mm. Available material is not adequate to give a reliable range of lengths of the tooth rows for the Cedar Creek specimens. Two lower jaws from the lower part of the Cedar Creek member and two from the middle part give a range in length of 6.8 mm. to 7.0 mm. for  $P_4$ - $M_2$ . The length of  $P^3$ - $M^2$  in No. 9092 is 9.0 mm., but the tooth row is distorted so that this measurement may be too large. The length of the P3-M2 of No. 9093 is 8.3 mm.

#### Palaeolagus haydeni Leidy

Palaeolagus haydeni LEDY, 1856, p. 89.

Referred specimens.—Cedar Creek member (lower): No. 9091; 25 upper and lower jaws; SW% sec. 12, T. 11 N., R. 54 W., Logan County.

Although specimens of Palaeolagus haudeni from

northeastern Colorado average slightly smaller than typical Nebraskan specimens, the Coloradan specimens are still within the size range of the species. The Coloradan specimens have a range in length of P3-M2 from 6.8 mm. to 7.8 mm. and a P4-M2 range from 6.0 mm. to 6.6 mm. These measurements afford a ready means of distinguishing this species from other northeastern Colorado species and are unreliable only in very young or very old specimens.

Palaeolagus haydeni is listed as occurring only in the lower part of the Cedar Creek member, where it does so in abundance. One specimen, however, from the upper part of the Horsetail Creek member seems to be referable to this species, and a few specimens occur near the base of the middle part of

the Cedar Creek.

Occasionally specimens are found that have an occlusal pattern like that of Palaeolagus burkei instead of P. haydeni but fall in the size range of P. haydeni. Inasmuch as these anomalies occur in the lower levels of the Cedar Creek in association with normal P. haydeni, it has been assumed that these large specimens are P. haydeni.

#### Palaeolagus burkei Wood

Palaeolagus burkei Wood, A. E., 1940, p. 325.

Type.-AMNH No. 8704; Leptauchenia beds of northeastern Colorado.

Referred specimens. — Cedar Creek member (middle): Referred specimens.—Cedar Creek member (middle):
No. 9088; anterior part of skull and associated left jaw with
P4-M3; E½ sec. 3, T. 11 N., R. 54 W., Logan County. No.
9089; anterior part of skull and associated lower jaws; NE½
sec. 3, T. 11 N., R. 54 W., Logan County.
Vista member: No. 9085; four fragments of lower jaws;
E½ sec. 12, T. 11 N., R. 54 W., Logan County.

Palaeolagus burkei is the most easily recognized species of Palaeolagus in northeastern Colorado and is especially distinctive in the characters of the skull and upper teeth (Wood, 1940, p. 325). Like the other species in this area, the teeth have a size range that is almost diagnostic. The range in length of P3-M2 is from 6.1 mm. to 6.8 mm., and that of P<sub>4</sub>-M<sub>2</sub> is from 5.0 mm. to 5.9 mm.

#### Megalagus turgidus (COPE)

Palaeolagus turgidus Cope, 1873b, p. 4. Megalagus turgidus, WALKER, 1931, p. 234.

Tupe.—AMNH No. 5635; Tertiary of Colorado.

Referred specimens.—Cedar Creek member: No. 9083; left maxillary; S½ sec. 7, T. 11 N., R. 53 W., Logan County. No. 9084; four lower jaws; NE½ sec. 3, T. 11 N., R. 54 W., Logan County.

This species is found throughout the Cedar Creek member.

# Order RODENTIA Bowdich, 1821 Family ISCHYROMYIDAE Alston, 1876

A considerable number of prosciurine specimens have been referred to Prosciurus, and caution has been used by all workers in naming new genera and species. The treatment accorded the prosciurines in this paper is the result of consideration of more than 70 specimens of which more than half were from northeastern Colorado. A new genus is named, and all the smaller specimens have been assigned, tentatively, to Prosciurus relictus.

Approximately 150 fragments of upper and lower jaws assignable to Ischyromys have been collected by University of Kansas field parties in northeastern Colorado. Of this number the stratigraphic position within the members is known for 85 of the

specimens.

Several specimens have been referred, tentatively, to Titanotheriomys.

#### Prosciurus relictus (COPE)

Plate 2, figure A; Figure 16

Paramys relictus COPE, 1873c, p. 3. Prosciurus relictus, Matthew, 1909, p. 105.

Type.—AMNH No. 5360; Tertiary of northeastern Colo-

Referred specimens.—Cedar Creek member (lower): No. 8340; right maxillary with P4-M3. No. 8341; left jaw with M1-M3. Both specimens from SW4 sec. 12, T. 11 N., R. 54

W., Logan County.

W., Logan County.
Cedar Creek member (middle): No. 8317; left jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8318; right jaw with P<sub>4</sub>-M<sub>2</sub>. No. 8321; right jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8323; left jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8322; right P<sup>4</sup>-M<sup>2</sup>. No. 8324; left jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8325; right jaw with M<sub>1</sub>-M<sub>2</sub>. Above seven specimens from W½ sec. 7, T. 11 N., R. 53 W., and E½ sec. 12, T. 11 N., R. 54 W., Logan County. No. 8326; right jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8327; left jaw with P<sub>4</sub>-M<sub>2</sub>. No. 8333; anterior part of skull with right and left M<sup>2</sup>-M<sup>3</sup>. No. 8345; anterior part of skull without teeth. Above four specimens from E½ sec. 3, T. 11 with right and left M-M-. No. 8343; afterior part of skilling without teeth. Above four specimens from E½ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8328; right maxillary with P4-M3. No. 8329; right jaw with P4-M3. No. 8330; left jaw with P4-M3. No. 8329; right jaw with P4-M3. No. 8330; left jaw with P4-M3. Above three specimens from SW¼ sec. 21, T. 11 N. R. 53 W., Logan County. Univ. Colorado Mus. No. 19850; two right lower jaws with P4-M3; W½ sec. 7, T. 11 N. R. 53 W. Logan County. T. 11 N., R. 53 W., Logan County.

Twenty-five upper and lower jaws of this species from northeastern Colorado and 28 upper and lower jaws from the Brule of Nebraska were available for

Enough material was collected from restricted levels and localities to give a good idea of variation in the teeth of *Prosciurus relictus* and to eliminate any doubt about association of the upper and lower teeth.

Variation in length of tooth row, individual teeth Table 6), and component parts of the teeth occurs, but there does not seem to be any correlation of size

variation with stratigraphic position.

The third upper premolar is peglike. The fourth premolar and the molars have well-developed protocones, incipient hypocones, well-developed anterior cingula, but weak or no posterior cingula. Cusps comparable to the parastyle on P4 tend to develop at the buccal end of the anterior cingula of the molars. The paracone, metacone, metaconule, and protoconule decrease in size in the order listed but all are distinct, with the exception of the metacone

and metaconule on M<sup>3</sup>. Some mesostyles have crests extending into the valley between the two lophs but never have crests uniting the mesostyle to either the paracone or metacone. The third molar has developed a heel by enlargement of the metacone at the postero-external angle of the tooth. On M<sup>3</sup> the mesostyle is united to the metaconule by a crest. The metacone maintains its union to the metaconule by a crest unless the metaconule is weak or absent, in which case the crest extends to the protoloph, joining it near the protocone.

The upper teeth of *Prosciurus relictus* may be distinguished from those of *P. vetustus* (Matthew) by two characters—relatively greater width and the number of "metaconules" present. When more specimens of *P. vetustus* are known, these distinctions may break down, but at present they seem valid. None of the specimens of *P. relictus* have anything that can be considered as a second or double metaconule. In size *P. vetustus* is intermediate between the smaller specimens of *P. relictus* and the larger specimens represented by the type.

The lower teeth of *Prosciurus relictus* have been figured and described (Woop, 1937, pp. 162, 168-169); therefore, only the variations seen in the present collection of specimens will be discussed. The mesostylid varies in position and attachment to the metaconid and entoconid, although the normal condition is separation from both metaconid and entoconid by notches. Mesostylid crests, if present, extend into the basin of the tooth and may be large. When large, the crests may unite with the hypolophulids. The completeness and strength of the hypolophulid on each tooth is subject to two common variations which are not the result of wear.

Some hypolophulids extend transversely across the tooth toward the ectolophid, being either well developed and united to the ectolophid or weak and failing to unite; others turn back toward the posterolophid and unite with that crest, or when weak fail to reach the crest. In some teeth the hypolophulid unites with both ectolophid and posterolophid. The anteroconid may or may not be present on the premolar, and likewise the ectostylids vary on the cheek teeth. The variations listed above are the most prominent and are the ones that could most easily be mistaken as characters that distinguish species.

That these specimens might represent three species has been seriously considered by me. By size the specimens may be segregated into three groups: the first—those the size of the type of *Prosciurus relictus* to which most belong; a second group—all small specimens with narrow teeth; and perhaps a third group—larger in size than the type specimen and having teeth relatively wider. As yet, I cannot (at least to my own satisfaction) correlate these size groups with other morphological variations or with stratigraphic positions. Furthermore, the same condition seems to exist among specimens from the Brule of Nebraska.

Specimen No. 8333 (Pl. 2, fig. A; Fig. 16) consists of the preorbital and interorbital parts of a skull. The nasal and lacrimal bones are lost; the premolars and first molars are missing; and the zygomata are lacking back of the maxillaries. Its size is comparable to that of *Glaucomys sabrinus* Shaw. The specimen has a remarkable resemblance in proportions to the skull of *Promylagaulus riggsi* described by McGrew (1941c, fig. 1). The skull

Table 6.—Measurements (in mm.) of Prosciurus relictus

	No. 833	3					No. 8328	1	No. 8340
Tooth row length at alveolus Premolar to incisor length Width of palate at P <sup>4</sup> Length of incisive foramina Width of incisive foramina Width of rostrum in front of zygomatic structure Height of skull at M <sup>2</sup> Antorbital width of frontals		Crown ler P <sup>4</sup> , antero P <sup>4</sup> , transvo M <sup>1</sup> , antero M <sup>1</sup> , transv M <sup>2</sup> , antero M <sup>2</sup> , transv M <sup>3</sup> , antero M <sup>3</sup> , transv	-posterio erse wid o-posteri verse wid o-posteri verse wid o-posteri	or length th or length dth or length dth or length dth or length		1.77 1.90 1.50 1.93 1.56 1.95 1.70		7.50 2.01 2.50 1.80 2.41 1.86 2.46 2.07 2.19	
	No. 8317	No. 8321	No. No. No. No.				No. 8330		lo. 850⁴
Crown length of P <sub>4</sub> -M <sub>3</sub> P <sub>4</sub> , antero-posterior length P <sub>4</sub> , transverse width of anterior lophid P <sub>4</sub> , transverse width of posterior lophid M <sub>1</sub> , antero-posterior length M <sub>1</sub> , transverse width of anterior lophid M <sub>1</sub> , transverse width of posterior lophid M <sub>2</sub> , antero-posterior length M <sub>2</sub> , transverse width of anterior lophid M <sub>2</sub> , transverse width of posterior lophid M <sub>3</sub> , antero-posterior length M <sub>3</sub> , transverse width of anterior lophid M <sub>3</sub> , transverse width of anterior lophid M <sub>3</sub> , transverse width of anterior lophid M <sub>3</sub> , transverse width of posterior lophid M <sub>3</sub> , transverse width of posterior lophid	7.10 1.77 1.14 1.68 1.65 1.50 1.65 1.95 1.56 1.83 2.25+	6.80 1.59 1.14 1.56 1.35 1.50 1.71 1.50 1.71 2.07 1.62 1.62	7.00 1.68 1.17 1.56 1.65 1.32 1.53 1.74 1.47 1.71 2.13 1.50 1.50	7.60 1.92 1.14 1.65 1.77 1.41 1.65 1.95 1.62 1.77 2.25 1.65 1.65	7.20 1.77 1.26 1.74 1.80 1.50 1.68 1.95 1.59 1.80 2.16+	6.66 1.62 1.26 1.53 1.62 1.38 1.56 1.80 1.53 1.68 2.07 1.56 1.41	6.60 1.50 1.08 1.50 1.44 1.32 1.50 1.68 1.53 1.65 2.01 1.56 1.32	6.60 1.62 1.26 1.62 1.62 1.44 1.56 1.80 1.56 1.74 2.10 1.50 1.53	6.60 1.53 1.26 1.59 1.53 1.44 1.62 1.80 1.71 2.10 1.50 1.44

a. Two specimens from the University of Colorado catalogued under this number.

is shallow vertically and has a short and wide rostrum, narrow palate, and long tooth row (Table 6).

Judging from the structure of the premaxillaries and the matrix in the nasal cavity, the nasal bones were large and heavy, extending as far back as the premolars and overlapping onto the frontals. Anteriorly they were slightly flared out laterally and possibly were flattened and turned downward.

The premaxillary bones, which constitute most of the anterior part of the rostrum, give the anterior part of the skull its characteristic short stubby appearance. Exclusive of the frontal process, the sutural union of the two bones to the maxillaries is essentially in one transverse plane. The frontal process is broad and blunt. Dorso-anteriorly, the inner edge of the bone turns upward to meet the nasal bone. Ventrally, the premaxillaries make up all of the lateral border of the incisive foramen. The median septum is large and heavy and, presumably, is composed of two processes of the premaxillary bones. Because of the short rostrum, the incisive foramina are crowded close to the incisors. No other foramina are discernible on the premaxillaries.

The incisors are heavy and directed ventromedially from each premaxillary. The anterior faces are flatly convex, and each lateral face meets at the rear of the tooth to form a roughly triangular

cross section, slightly longer than wide.

Both maxillary bones are complete, except that the zygomatic processes may have lost their extreme Antero-ventrally, the maxillaries form the posterior border of the incisive foramina. palate is narrow, and the suture between the maxillaries and palatines forms a bow at the anterior end of the second molars. The zygomatic root rises abruptly at the anterior end of the tooth row, and the zygomatic plate shows no forward inclination. Laterally the zygomatic process extends outward and backward, terminating in a slender point. The ventral surface of the process has a groove which is presumed to be the attachment scar for the lateral masseter muscle. At the medial end of the anterior ridge forming the attachment scar, a small pro-The infraorbital foramen is tuberance is visible. roughly oval in shape and relatively large in diameter. The infraorbital canal is elongate anteroposteriorly, and the orbital opening lies above the tooth row in the orbit. The maxillary forms the anterior and ventral borders of the orbit, and internally, the floor and a small part of the median The palatine process is large, because of the relatively large teeth, and resembles Ischyromys in this respect. The part composing the medial wall of the orbit is limited to a triangular plate of bone rising from the floor of the orbit and extending upward between the lacrimal and the frontal bones. In the ventro-posterior part of the orbit the maxillary joins the frontal bone and encloses the sphenopalatine foramen. Posterior to this a second foramen is present in the maxillary just anterior to the

palatomaxillary suture. M²-M³ are similar to those described previously. Comparison of this specimen with the type (a maxillary fragment with teeth) of *P. vetustus* shows no differences worth noting in the maxillary.

The palatine bones are well preserved, lacking only the pterygoid processes. The maxillary process of the palatine bone is united to the maxillary bone by a suture that courses along the lateral border of the palate from M³ to the anterior end of M² where the suture becomes highly sinuous and crosses the palate to the mid-line. Thus, the union of the palatines with the maxillaries makes a suture in the

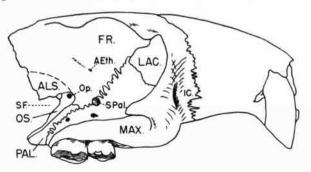


FIGURE 16.—Prosciurus relictus (COPE). No. 8333. Lateral view of right side of skull showing structures in the orbital area. ALS, alisphenoid. FR, frontal. LAC, lacrimal. MAX, maxillary. OS, orbitosphenoid. PAL, palatine. AEth, anterior ethmoid foramen. Op, optic foramen. SPal, sphenopalatine foramen. SF, sphenoidal fissure. IC, infraorbital canal. Approximately × 4.

shape of a U with the base forward on the palate. The double posterior palatine foramina pass through the palatine bone, with the anterior foramen much larger than the posterior one. The rear of the palate is emarginate, each palatine bone having its median edge terminating opposite the mid-point of M³. There is no evidence of more than an incipient palatine pit posterior to M³. The orbital process of the palatine is a thin sliver of bone extending up between the maxillary and orbitosphenoid where it meets the frontal and plays little part in forming the floor of the orbit. Posteriorly, the palatine expands downward behind the maxillary and beneath the orbitosphenoid (?presphenoid).

In dorsal view, the frontal bone is twice as wide anteriorly as it is posteriorly, resembling the form seen in *Aplodontia* and *Paramys*. The anterior dorsal border is more or less transverse to the long axis of the skull, but the sutures curve forward slightly at each side. The antero-lateral "wing" of the frontal curves downward on the side to meet the maxillary and the lacrimal to form the antero-dorsal border of the orbit. An incipient postorbital process projects outward from the dorsal surface of the frontal bone. Preservation around the lacrimal canal is poor, but judging from the size of the lacrimal, it is doubtful that the frontal bone assisted in the composition of that canal. The orbital plate of

the frontal makes up the posterior part of the inner wall of the orbit and contributes to the formation of at least the upper part of the posterior orbital wall. The orbitosphenoid-frontal suture borders the optic foramen. Ventrally, the orbital plate extends to the orbital process of the maxillary bone and forms the upper border of the sphenopalatine foramen. The plate terminates ventrally as a tongue of bone extending downward between the orbitosphenoid and maxillary bones to meet the orbital process of the palatine bone. About 2 mm. above the sphenopalatine foramen the orbital plate is pierced by the anterior ethmoid foramen, and posterior to it is a groove in the plate which served as a partial passageway for the nerve or blood vessel that coursed across the inner wall of the orbit. Posteriorly, there is no trace of a suture between the dorsal surface of the frontal and the parietal.

Antero-lateral to the "wing" of the frontal is a notch in the border of the orbit. This is not natural, and, although it is now lost, the lacrimal probably fitted into this space and formed the dorsal part of the anterior wall of the orbit.

The orbit is large and open but, unlike the orbit of the squirrels, has a small part formed by bones other than the frontal, maxillary, and lacrimal.

In this specimen the alisphenoid seems to form no more than the postero-ventral wall of the orbit. The position of the alisphenoid-frontal suture has been tentatively determined (Fig. 16).

The orbitosphenoid bone makes up little of the orbital wall and occupies a narrow part of the postero-ventral area of the orbit between the alisphenoid, palatine, and frontal. The optic foramen is small.

Comparison of No. 8333 with maxillaries of Prosciurus relictus containing good teeth leaves little doubt as to the identity of this specimen; similarity is shown in teeth, palatal structure, and zygomatic root structure. Also, enough upper and lower teeth of P. relictus have been found in the area to remove any doubt as to association.

A poorly preserved, smaller, but similar fragment of skull, No. 8345, lacks arches and teeth. It has

been tentatively referred to Prosciurus.

#### PELYCOMYS, new genus

Type species.—Pelycomys rugosus, new species. Distribution.—Chadronian and Orellan beds of northeastern Colorado.

Diagnosis.—Incisors laterally compressed; lower cheek teeth subtrigonal to subrhombic in shape; principal cusps rounded and large; trigonid large, with metalophulid II essentially complete; hypolophulid well developed and separate from posterolophid; metastylid small and fused to metaconid or united to it by a crest; entoconid separated from posterolophid and metastylid by notches.

# Pelycomys rugosus, new species

Figure 17

Holotype. — Part of right jaw with M<sub>1</sub>-M<sub>3</sub>, No. 8343, Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist.

Geological age and locality.—Silts of Chadronian age in the Horsetail Creek member of the White River formation at "Flat Top," a prominent butte, in sec. 1, T. 10 N., R. 54 W., Logan County, Colorado.

Diagnosis.—Differs from Pelycomys placidus in having trigonids wider; mesoconids and buccal mesolophids weaker or absent; hypoconids larger; metastylids of M1-M2 higher on sides of metaconids; and entoconids smaller. Anterior and posterior arms (anterolophid and metalophulid II) of protoconids reaching metaconids and hypolophulids extending across the basins to ectolophids. M3 is relatively larger than that of P. placidus.

Description.—Little of the jaw is preserved, but the specimen indicates that the jaw is relatively deeper and shorter than that of Prosciurus relictus. The length of the cheek-tooth series (Table 7) in this new species is slightly less than that of Cedromus wardi and PProsciurus jeffersoni, and almost twice the length of the tooth row of Prosciurus relictus. The masseteric scar is weak, more like that of Prosciurus than Cedromus. The teeth of the type specimen are moderately worn.

The base of the incisor indicates that this tooth was compressed laterally, much more so than in

Prosciurus.

None of the cheek teeth have high cusps, but, like those of *Prosciurus*, the metaconids are highest. The protoconids and entoconids are of equal height, and the hypoconids, although they are expanded and larger than the other cusps, are the lowest in Compared with those of Prosciurus, the mesoconids, posterolophids, and entoconids are reduced. Unlike *Prosciurus*, the metaconids and hypoconids are not compressed antero-posteriorly. The trigonid pits of the molars are enclosed by the anterolophid and the metalophulid II. Deep notches separate the entoconids from the metastylids, and shallower notches separate the entoconids from the posterolophids. Large and flat-floored transverse valleys extend from the ectolophids to the buccal margins of the teeth. The buccal mesolophids are

Table 7.—Measurements (in mm.) of Pelycomys rugosus

	No. 8343
Crown length of M <sub>1</sub> -M <sub>3</sub>	9.40
M1, antero-posterior length	2.85
M <sub>1</sub> , transverse width of anterior lophid	2.55
M <sub>1</sub> , transverse width of posterior lophid	2.73
Mo, antero-posterior length	3.20
M <sub>2</sub> , transverse width of anterior lophid	3.00
M <sub>2</sub> , transverse width of posterior lophid	3.08
M <sub>3</sub> , antero-posterior length	4.18
M <sub>3</sub> , transverse width of anterior lophid	3.05
M <sub>3</sub> , transverse width of posterior lophid	2.71

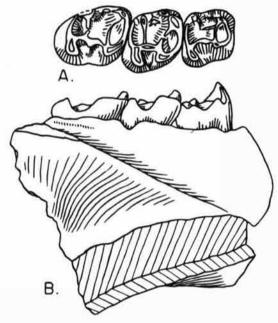


FIGURE 17.—Pelycomys rugosus, n. gen. and sp. No. 8343. (A) Occlusal view of right  $M_1$ - $M_3$ . (B) External view of right jaw with teeth. Approximately  $\times$  5.

small. The first molar is the smallest, and the third molar is the largest.

On the first molar the anterolophid uniting the protoconid and metaconid is large and similar in shape to that seen on the *Prosciurus* molar. The metalophulid II seems weak and gives the appearance of having been a mutual development from both cusps. The metastylid is small and arises as an attenuated cuspule on the postero-lingual side of the metaconid. A weak ridge extends from the metalophulid II to the hypolophulid closing off the notches between the metaconid and entoconid from the central basin. A small cuspule is developed in the posterior end of this ridge anterior to its union with the hypolophulid. The mesoconid is no more than a swelling in the ectolophid, and has no buccal mesolophid. The hypolophulid is weak.

The trigonid of the second molar is similar in all respects to that of M<sub>1</sub>, except that it is not so high. As on M<sub>1</sub>, a weak ridge extends antero-posteriorly through the central basin, blocking the base of the deep notch between the metaconid and entoconid. There is evidence of a small cuspule on this ridge opposite the notch. The mesoconid and buccal valley between the protoconid and hypoconid is similar to that on M<sub>1</sub>. The hypolophulid is complete and united to the mesoconid.

M<sub>3</sub> has a trigonid similar to that of M<sub>2</sub> but with the metastylid separated from the metaconid by a small notch. The antero-posterior ridge in the central basin of this tooth extends from the metastylid to the median border of the entoconid. The progressive lingual shift of the anterior end of this

ridge may be seen in the teeth of this specimen as one observes successively the first, second, and third molars. Although considerable attention has been devoted to this ridge in the description of these teeth, possibly the feature is an individual characteristic and one which should not be relied upon at present to distinguish this species. The mesoconid of the third molar is the only one in the series of molars to show development similar to anything seen in other prosciurine-like rodents. A poorly developed mesolophid extends into the buccal valley between the protoconid and hypoconid. hypolophulid unites with the ectolophid posterior to the mesoconid. The part of the ectolophid posterior to the hypolophulid does not turn buccally toward the hypoconid as is the case in M1-M2, but extends straight back to unite with the posterolophid. The hypolophulid of this tooth is divided by a notch and gives the impression of having developed from the entoconid and ectolophid, respec-This suggests the mode of origin of the hypolophulid in the prosciurine group. Although the enamel surfaces of the entoconid and posterolophid are damaged, the posterolophid seems to be made up of one cusp, and only a notch separates this element from the entoconid.

# Pelycomys placidus, new species

Figure 18

Holotype.—Part of left lower jaw with M<sub>1</sub>-M<sub>3</sub>, No. 8334, Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist.

Referred specimens.—No. 8335; right lower jaw with  $M_2$ , No. 8336; left lower jaw with  $P_4$ - $M_2$ . Univ. Colorado Mus. No. 19859; right lower jaw with  $P_4$ - $M_2$ . All specimens from type locality except No. 19859 which is from the center of sec. 3, T. 11 N., R. 54 W., Logan County.

Geological age and locality.—Silts of Orellan age in the Cedar Creek member of the white River formation in W½ sec. 7, T. 11 N., R. 53 W., Logan County, Colorado.

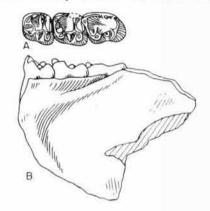
Diagnosis.—Differs from Pelycomys rugosus in having trigonids narrower; mesoconids and buccal mesolophids better developed; hypoconids smaller; metastylids lower on sides of metaconids; entoconids larger; and metalophulid II of molars weaker and lower than anterolophid, and complete.

Description.—The incisors of Pelycomys are distinguished by greater compression laterally than in either Cedromus or Prosciurus. No. 8336 has the best preserved incisor of any of the specimens and shows that the internal face of the tooth is flat, the anterior face is rounded, and the external face is gently curved toward the posterior border of the internal face.

P<sub>4</sub> of the referred specimens has the trigonid damaged, but it can be ascertained that the anterolophid between the protoconid and metaconid was absent and that the metastylid was connected to the side of the metaconid by a crest. The mesoconid is not well developed, and the buccal mesolophid is absent. The entoconid is high and is separated from the posterolophid and metastylid by narrow,

The ectolophid is united to the deep notches. hypoconid.

All the molars have the protoconid and metaconid spaced far apart and united by a heavy anterolophid. The metastylid is on the side of the meta-



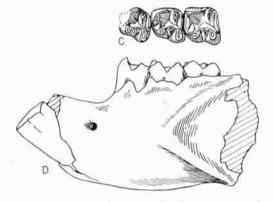


FIGURE 18.—Pelycomys placidus, n. gen. and sp. No. 8334: (A) Occlusal view of left M<sub>1</sub>-M<sub>3</sub>. (B) External view of left jaw with teeth. 8336: (C) Occlusal view of left P<sub>4</sub>-M<sub>2</sub>. External view of left jaw with teeth. Approximately  $\times$  3.

conid on all three molars and is united to the metaconid by a small crest. Because of the narrower trigonid, the teeth appear more like those of Prosciurus than do the teeth of Pelycomys rugosus. The molars differ from one another in the following respects. On M, the metalophulid II is a weaker ridge than the anterolophid but is as high; and between them and the protoconid and metaconid, they form the trigonid pit. The entoconid is as high as the protoconid and is separated from the metastylid and posterolophid by narrow, deep notches. The mesoconid is well developed and has a heavy buccal mesolophid extending into the valley or embayment between the protoconid and hypoconid. The hypolophulid on M, is complete before wear and unites with the ectolophid and, from the evidence of the referred specimens, is obliterated medially after wear. The posterolophid is well developed and has a large cusp near its union with the hypoconid. The hypoconid on M, is well developed but somewhat less so than in the other molars.

On M<sub>2</sub> the metalophulid II tends to be weaker than in M<sub>1</sub> and is almost lost on the metaconid side. The entoconid, mesoconid, hypolophulid, and posterolophid are similar to those structures on the first molar. The hypoconid is even larger and more

prominent on M, than on M,

The third molar differs from the other two in many ways. The metalophulid II is incomplete on the metaconid side. The entoconid is not so high as the entoconids on the other molars, and only shallow notches separate it from the metastylid and posterolophid. The mesoconid is larger than the entoconid, and the part of the ectolophid between it and the protoconid is weak. Likewise, the part of the ectolophid between the mesoconid and hypoconid is incomplete, but this may be peculiar to the type specimen, which otherwise would have a complete but weak and low ectolophid. The hypolophulid seems to be absent. On M<sub>3</sub>, the hypoconid reaches its greatest development and forms a massive heel as high as the metaconid, which makes up

Table 8.—Measurements (in mm.) of Pelycomys placidus

	No. 8334	No. 8335	No. 8336	No. 19859a
Crown length of M <sub>1</sub> -M <sub>3</sub>	8.91	2.47473	0.0.00	F1154
I, antero-posterior length	2015/6		3.25	2.414.0
I, transverse width	1412 (4.9)	4 4 4 4	1.80	597474
P4, antero-posterior length	0.79%	2/4/5/2	2.80	2.44
P. transverse width of anterior laphid	72.000	7.000	2.17 <sup>b</sup>	2.00+
P4, transverse width of posterior lophid		5.5.5.5	2.77	2.50
M <sub>1</sub> , antero-posterior length M <sub>1</sub> , transverse width of anterior lophid	2.75	F. F. F. S.	2.80	2.50
M1, transverse width of anterior lophid	2.35	5553	2.50	2.30
M <sub>1</sub> , transverse width of posterior lophid	2.70	107.61	2.94	2.50+
M <sub>2</sub> , antero-posterior length	2.90	3.15	3.15	2.80
M <sub>2</sub> , transverse width of anterior lophid		2.70	2.81	2.50
M2, transverse width of posterior lophid	2.60 +	2.86	2.99	2.65
Mo antero-nosterior length	3.85	5050		
M <sub>3</sub> , transverse width of anterior lophid	2.66	45.44		25,00
M <sub>3</sub> , transverse width of posterior lophid	2.25+		5555	11000
43, dansverse width of posterior toping	~.~.	5.555	#1.8 · # (b.)	

a. University of Colorado Museum.

b. Estimated.

the whole rear of the tooth. An arm from the hypoconid reaches forward to the protoconid enclosing the large mesoconid buccally.

The size of the cheek teeth is given in Table 8.

#### Pelycomys sp.

Referred specimens.—AMNH No. 8750; left lower jaw with P<sub>4</sub>-M<sub>3</sub>; Cedar Creek beds, northeastern Colorado (fide Wood, A. E., 1937).

Woon, A. E., 1937). Cedar Creek member (lower): No. 8971; right lower jaw with P<sub>4</sub>-M<sub>3</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan

County.

Cedar Creek member (middle): No. 8344; a first or second left upper molar; SW¼ sec. 21, T. 11 N., R. 53 W., Logan County.

Wood (1937, p. 170) identified the American Museum specimen as *Prosciurus* cf. *P. saskatchewaensis* (Lambe). This specimen and No. 8971 are smaller than individuals of *Pelycomys* already described and are larger than large individuals of *Prosciurus relictus*. The narrowness of the incisors, completeness of the metalophulid II, thickness of the metaconids, and small size of the metastylids suggest that the two specimens are referrable to the genus *Pelycomys*. The specimens may be *Pelycomys placidus* but possibly they and the University of Colorado Museum specimen No. 19859, which is referred to *Pelycomys placidus*, are an unnamed species.

No. 8344 is large, 2.7 mm. long and 3.1 mm. wide. There is a parastyle on the buccal end of the anterior cingulum, and a definite hypocone and protoconule are present. Whether or not it is referable to *Pelycomys* remains to be decided but it is a prosciurine tooth comparable in size with the lower teeth of this genus.

Discussion.—The differences in the teeth of Pelycomys rugosus and Pelycomys placidus are the basis for making two species in this genus. Pelycomys placidus has a larger talonid basin than P. rugosus. This feature is especially noticeable in M<sub>3</sub> of P. placidus which does not have the basin worn, and shows that the absence of crests and lophids from the basin is real. Structurally the enlargement of the basin is seen as a trend that parallels the enlargement of the basin in Prosciurus. In Prosciurus the enlargement is accomplished by a diagonal elongation of the teeth and loss of the metalophulid II, whereas in Pelycomys enlargement is at the expense of metalophulid II and the hypolophulid.

In my opinion *Pelycomys* belongs in the subfamily Prosciurinae (Wilson, 1949b, pp. 77, 92) along with *Prosciurus* and *Sespemys*. Further consideration of this genus and its relations to the genera *Prosciurus* and *Cedromus* will be found in the discussion of *Cedromus*.

#### Ischyromys typus Leidy

Ischyromys typus LEDY, 1856, p. 89.

Referred specimens.—Cedar Creek member (lower and middle): No. 9058; anterior part of skull, mandible, and

fragments of skeleton; sec. 28, T. 11 N., R. 53 W., Logan County. No. 9075; left jaw with  $P_4$ - $M_3$ ; SE¼ sec. 31, T. 12 N., R. 54 W., Logan County. No. 9054; right  $M_1$ - $M_3$ ; SE¼ sec. 7, T. 11 N., R. 53 W., Logan County. No. 9056; left  $P_4$ - $M_2$ ; E½ sec. 3, T. 11 N., R. 54 W., Logan County.

Except for eight specimens, all the *Ischyromys* material (more than 100 specimens) has been referred to this species. Nearly all the specimens were collected in pink, sandy silts or silts intimately associated with the sandy silts, indicating to me that

the animal inhabited the valley floor.

A trend seen from a study of the vertical distribution of these specimens is increasing length of P4-M<sub>3</sub> and a change in the shape of the teeth. As typified by No. 9058, specimens found in the lower part of the Cedar Creek member have a length of P4-M3 less than 15 mm. and relatively narrow teeth. In the middle part or silty phase of the Cedar Creek member, the specimens, as exemplified by No. 9075, have a length of  $P_4$ - $M_3$  of between 15 and 16 mm. At this level the cheek teeth are narrow or quadrate, and M, and M, are relatively larger than those found in the lower beds. At the top of this part of the section, specimens, such as Nos. 9054 and 9056, have a length of P<sub>4</sub>-M<sub>3</sub> that is more than 16 mm. but otherwise resemble the smaller specimens of Ischyromys typus. In length of lower dentition, these and other specimens from this level exceed that of the type of I. pliacus and other specimens referred to it. Although these differences have been presented as representing stratigraphic groups, the divisions are not clear-cut. There are variations within each group, but the mean length of the cheek teeth is increasing. More collecting and study is necessary before this apparent increase in size (as shown by increased length of tooth row') and change in the shape of the teeth are satisfactorily demonstrated to be the change of a single phyletic

In this apparent chronocline the smaller teeth resemble specimens referred by Wood to *Ischyromys* typus, and the larger teeth resemble those referred by him to I. pliacus, which could be interpreted as indicating that I. pliacus is an end product of the I. typus line. If part of the material assigned to I. pliacus by Wood is really part of the I. typus chronocline, then the remainder of the large specimens, such as those from Pipestone Springs and Thompson Creek referred to I. pliacus by Wood (1937, p. 190), represent a distinct species. Bar-BOUR & STOUT (1939, pp. 30-32) offer evidence on the stratigraphic occurrence of I. pliacus which supports the views that have been presented here. Furthermore, their evidence suggests that the type specimen of I. pliacus belongs to the I. typus chronocline rather than to the large unnamed species.

Attention is directed here to the type locality of Ischyromys pliacus Troxell. Troxell (1922, p. 124) gave the geological age and locality as middle Oligocene, Cherry Creek, Colorado. Wood (1937, p. 190) gave the level as Cedar Creek. I supposed

that Troxell wrote Cherry Creek when he meant Cedar Creek, but Dr. Joseph T. Gregory investigated the records at Yale University and stated (letter, April 15, 1950):

The type of *Ischyromys pliacus* Troxell was collected by O. C. Marsh on August 22, 1870 and bears the label Cherry Creek in his hand. According to the map of the route of the 1870 expedition (Schuchert and Levene, "O. C. Marsh, Pioneer in Paleontology," p. 106) the party camped on Lodge Pole Creek north of Fort D. A. Russell, NW of Cheyenne, Wyoming that day. They had come through the Goshen Hole area, up Horse Creek, during the preceding days, and had camped at the mouth of a Cherry Creek, tributary to Horse Creek, on August 20. . . . this data would certainly exclude the Cedar Creek, Colorado, area as the type locality.

#### Ischyromys troxelli Wood

Ischyromys troxelli Woop, A. E., 1937, p. 191.

Referred specimen,—Horsetail Creek member: No. 9126; right M<sub>2</sub> in fragment of jaw; NE¼ sec. 31, T. 11 N., R. 56 W., Weld County.

This tooth has its antero-posterior length shorter than its width (3.7 mm. × 3.9 mm.), a short anterior protoconid arm, and its median valley open internally. Except for its larger size and relatively greater width, it resembles the teeth referred to *Titanotheriomys*, No. 9113, from the lower part of the Horsetail Creek member in Logan County.

Woon (1937, p. 191) reports the species from the

Cedar Creek beds.

#### Titanotheriomys cf. T. veterior (MATTHEW)

Referred specimens.—Horsetail Creek member: No. 9043; left  $P_4$ - $M_2$ ; NE¼ sec. 8, T. 11 N., R. 54 W., Logan County. No. 9052; right  $M_2$ - $M_3$ ; W½ sec. 30, T. 11 N., R. 51 W., Logan County. No. 9053; right  $P_4$ - $M_3$ ; sec. 28, T. 11 N., R. 53 W., Logan County. No. 9106; left  $P_4$ - $M_2$ ; W½ sec. 29, T. 11 N., R. 53 W., Logan County.

In size and pattern these specimens are close to *Titanotheriomys veterior*, the only difference being slightly longer lophids. These specimens were not compared with "*Colotaxis cristatus*" Cope (1873a, p. 1), but the size given by Cope for the type is slightly greater than in our specimens.

#### Titanotheriomys? sp.

Referred specimens.—Horsetail Creek member: No. 9113; left M<sub>1</sub>-M<sub>2</sub>; W½ sec. 9, T. 10 N., R. 51 W., Logan County. Cedar Creek member (lower): No. 9042; right P<sub>4</sub>-M<sub>2</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County. No. 9044; left P<sub>4</sub>-M<sub>1</sub>; locality same as No. 9042.

No. 9113, from the Horsetail Creek member, is the size of a small individual of *Ischyromys typus* but is tentatively assigned to this genus because of the weak anterior protoconid arm and posterior cingulum.

The two specimens from the lower part of the Cedar Creek member are intermediate in size between the specimens compared with *Titanotheriomys veterior* and the small individuals of *Ischyromys typus*. The fourth lower premolars are narrower, relatively, than those in *I. typus*, and the

tooth row is estimated to be approximately 14 mm. in length. No. 9044 has a posterior cingulum on  $M_{\scriptscriptstyle 1}$  consisting of three distinct cuspules, of which the most external is the largest.

# Family EOMYIDAE Depéret & Douxami, 1902

#### Adjidaumo minutus (COPE)

Gymnoptychus minutus Cope, 1873b, p. 6. Adjidaumo minutus, HAY, 1899, p. 253.

Type.—AMNH No. 5362; middle Oligocene of Colorado (fide Woop, A. E., 1937).

Referred specimens.—Cedar Creek member (lower): No. 8241; left jaw with  $M_1$ - $M_2$ ; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County. No. 8242; left jaw with I,  $P_4$ - $M_3$ ; N½ sec. 33, T. 11 N., R. 53 W., Logan County. No. 8243; right jaw with  $P_4$ - $M_1$ ; SE¼ sec. 17, T. 11 N., R. 65 W., Weld County.

Nos. 8242 and 8243 are similar to the type specimen in size and occlusal pattern. No. 8241 differs from the type in being smaller and in having shorter mesolophids.

## Adjidaumo sp. (Small form)

Referred specimens.—Horsetail Creek member: No. 9101; anterior part of right jaw lacking teeth; W½ sec. 29, E½ sec. 30, T. 11 N., R. 53 W., Logan County. No. 9395; right upper cheek tooth; SE¼ sec. 1, T. 10 N., R. 54 W., Logan County.

Neither one of these two specimens is so large as the corresponding parts in specimens of Adjidaumo minutus; probably they are some other species. The jaw fragment is lighter and has a shorter diastema than does the type specimen of Adjidaumo minimus (MATTHEW) from the Chadronian beds at Pipestone Springs. The antero-posterior length of the cheek tooth is 1.2 mm., and its transverse width is 1.4 mm. Both the anterior and posterior cingula are well developed and extend across the face and rear of the tooth to unite with the paracone and metacone, respectively.

#### Paradjidaumo trilophus (COPE)

Gymnoptychus trilophus COPE, 1873b, p. 6. Paradjidaumo trilophus, WOOD, A. E., 1937, p. 244.

Type.—AMNH No. 5401; middle Oligocene, Cedar Creek of Colorado (fide Woop, 1937).

Referred specimens.—Horsetail Creek member: No. 9791; left jaw with I, P<sub>4</sub>-M<sub>2</sub>; E½ sec. 30, T. 11 N., R. 53 W., Logan County.

County.

Cedar Creek member (lower and middle): Nos. 8244-8246; left jaws with P<sub>4</sub>-M<sub>2</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County. No. 8249; right maxillary with P<sup>4</sup>-M<sup>2</sup>; E½ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8250; right jaw with I, P<sub>4</sub>-M<sub>2</sub>; E½ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8253; left jaw with I, P<sub>4</sub>-M<sub>1</sub>; SE¼ sec. 17, T. 11 N., R. 65 W., Weld County. No. 8254; left jaw with P<sub>4</sub>-M<sub>3</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County. Univ. Colorado Mus. No. 19860; right jaw with P<sub>4</sub>-M<sub>2</sub>; locality same as No. 8254. No. 8255; left jaw with P<sub>4</sub>-M<sub>3</sub>; SW¼ sec. 21, T. 11 N., R. 53 W., Logan County.

More than a dozen specimens of this species were collected in northeastern Colorado, and all compare closely with the type specimen with the exception of Nos. 8244-8246 which are slightly smaller. A comparison of the group with 21 specimens from Sioux County, Nebraska (Nos. 548-565) shows agreement in pattern and size range with exception of the three specimens mentioned.

#### FAMILY SCIURIDAE GRAY, 1821

#### Cedromus wardi Wilson

Cedromus wardi Wilson, 1949, p. 29.

Type.—Univ. Colorado Mus. No. 19808; Cedar Creek member (lower), SW¼ sec. 12, T. 11 N., R. 54 W., Logan County, Colorado.

Referred specimen.—No. 8338; right jaw with M<sub>1</sub>-M<sub>3</sub>; E½ sec. 3, T. 11 N., R. 54 W., Logan County.

Field records show that No. 8338 probably came from the lower part of the Cedar Creek member. The tooth pattern, size of the teeth, and masseteric fossa of this specimen are like that of the type, but the jaw is larger and heavier, being 10 instead of 8 mm. deep at M<sub>1</sub>.

#### Cedromus? sp.

Plate 2, figures B-C; Figure 19

Referred specimens. — Cedar Creek member (middle): Univ. Colorado Mus. No. 19852; fragment of left maxillary with P<sup>4</sup>-M<sup>1</sup>; W½ sec 7, T. 11 N., R. 53 W., Logan County. Cedar Creek member (upper): No. 8342; damaged skull with right P<sup>3</sup>-M<sup>3</sup>; NE¼ sec. 3, T. 11 N., R. 54 W., Logan County.

These two specimens are provisionally assigned to *Cedromus*. Although I am personally convinced that the association of this material with the lower jaws and teeth of *Cedromus* is correct, the significance of the association is too important to make anything other than a provisional assignment until an actual occlusal association is found.

No. 8342 is an incomplete skull consisting of fragmentary right and left maxillary and palatine bones, right alisphenoid, fused basisphenoid and basioccipital, supraoccipital, exoccipital, mastoid, and parietal bones, which surround a brain case. Both auditory bullae are present but weathered.

In length the posterior part of the skull exceeds that of *Sciurus carolinensis* and is almost as wide and deep, but the brain case lacks the inflated appearance of Recent sciurids (Table 9). The palate is wide. The basicranial-facial axis is bent.

Both maxillary bones have only the palatal and orbital parts preserved. The short, small infraorbital canal lies above P<sup>3</sup>-P<sup>4</sup>. The zygomatic root originates above P<sup>4</sup> but is too damaged to preserve any details of the zygomatic plate. Because the suture between the maxillary and premaxillary bones lies fairly close to the anterior end of the tooth row, the zygomatic plate probably was not inclined forward to any great extent. The maxillary fragment, No. 19852, shows more of the zygomatic structure; the root seems to be wide and nearer a horizontal position. Both specimens, however, have enough of the zygomatic structure preserved to show that it

was much more sciurid-like than prosciurine-like. The incisive foramina probably did not extend back to the suture between the maxillaries and the premaxillaries. The maxillary bone is missing from most of the internal wall of the orbit because of damage, but it is present on the orbital floor. Below the posterior end of the infraorbital canal a small foramen leads into the bone. As a whole, the orbital process of the maxillary resembles that of Cynomys, but the part bordering the sphenopalatine canal is higher on the internal wall of the orbit. The palatal processes of the maxillaries produce a broad, flat plate with the suture between the two bones deeply incised.

The palatine bones are represented by the incomplete palatal, orbital, and pterygoid processes. The palatal processes are a continuation of the smooth maxillary part of the palate, and the suture between these bones passes forward along the inner side of M3 and, curving toward the mid-line, forms a rounded are that extends forward to the anterior end of M2. The canal for the palatine artery and nerve has two openings, both on the palatine bone, similar to those seen in Sciurus. An extraordinarily large palatine pit, which opens laterally, lies behind The orbital process of the palatine is similar to that in *Cynomys*. Like the maxillary, this process is damaged, and the full extent of the bone cannot be determined. A small fragment of the frontal bone meets the orbital process, and both bones together with the maxillary enclose the spheno-palatine foramen.<sup>23</sup> A small foramen lies posterior to the sphenopalatine foramen and leads into the palatine bone. The pterygoid process resembles the pterygoid process seen in Sciurus but lacks the ridges that extend forward from the pterygoid bone onto the palatine.

Only the lower part of the alisphenoid bone is preserved. The ventral wing flares outward and is in contact with the palatine and pterygoid bones. There is a large masticatory foramen, similar to that seen in *Cynomys*, in the center of this wing. The buccinator foramen lies back of the ventral wing and is just a groove, as in *Cynomys*, or, if damaged, was roofed over by a bar of bone. The alisphenoid turns sharply upward at its posterior end, and, combined with the wall of the basisphenoid and a notch in the auditory bulla, it forms a pit. This pit is not too well preserved, but the usual foramina of this area seem to be concentrated in it. The foramen ovale appears to be separated from the lacerate (median) foramen by a bar of bone.

The auditory bullae are ossified and firmly attached to the skull. In over-all appearance they resemble those of *Sciurus* but differ in having the

notches in the antero-medial angle larger, in having

<sup>23.</sup> In Ischyromys and Heliscomys the sphenopalatine foramen occupies a similar position. WILSON (1949, p. 38), however, found the foramen to be entirely enclosed by the maxillary bone in the comyids. In Prosciurus the foramen is between the frontal and maxillary bones, and in most sciurids the foramen is between the palatine and maxillary bones.

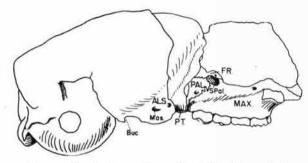


FIGURE 19.—Cedromus? sp. No. 8342. Lateral view of right side of skull showing structures in the orbital and basicranial area. FR, frontal. MAX, maxillary. PAL, palatine. ALS, alisphenoid. PT, pterygoid. Buc, buccinator foramen. Mas, masticatory foramen. SPal, sphenopalatine foramen. Approximately × 1.8.

the posterior ends laterally compressed, and in being less inflated. The lack of inflation in the bullae makes the foramina in this area appear large. The stylomastoid, jugular, and hypoglossal foramina are prominent but otherwise not different from the condition seen in *Sciurus*. Possibly there was a rather large stapedial foramen.

The basisphenoid and basioccipital bones are

fused and appear like those of Sciurus.

The occipital region of the skull is sciurid-like. The occipital plate is inclined forward but has neither the inflated appearance of *Sciurus* nor the concave shape of *Marmota*.

The mastoids are more pointed at their upper ends than those of *Sciurus*, and their ventral borders are accentuated by grooves that pass to the stylomastoid foramina.

The supraoccipital bone is pointed at its top, and a crest runs along the mid-line from the foramen magnum to the peak.

Table 9.—Measurements (in mm.) of Cedromus? sp.

	No. 8342	No. 19852
Crown length of P <sup>3</sup> -M <sup>3</sup> P <sup>3</sup> , antero-posterior length	10.9	
P <sup>3</sup> , antero-posterior length	1.2	0,0,00
r, transverse width	1.9	1978
r', antero-posterior length	2.6	2.7
P <sup>4</sup> , transverse width	3.0	3.0
M <sup>1</sup> , antero-posterior length	2.4	2.7
M <sup>1</sup> , transverse width	2.9	3.2
M <sup>2</sup> , antero-posterior length	2.4	
M2 transverse width	0.1	2/3/2/3
M°, antero-posterior length	2.0	51.51.515
M³, transverse width	3.0	51551

a. University of Colorado Museum.

The occipital condyles are low on the sides of the foramen magnum and, although the bottom of the foramen is damaged, do not appear to extend along it as in *Sciurus*. The paraoccipital processes stand away from the bullae, a feature in common with primitive rodents, but not with most Recent sciurids. The large foramen magnum is acute at the top, and it may be described best as five-sided in outline instead of round or trianguloid.

The parietals are incompletely preserved; but from the evidence of the suture marks on the brain cast, it is thought that, although the frontal-parietal suture was bowed slightly posteriorly, the frontal bone was not set within the dorso-lateral walls of the parietals as in *Sciurus*. There is no evidence of an interparietal bone. The temporal crests are lyrate and are almost united at the posterior end of the parietals. A lambdoid crest is present.

The squamosals are not preserved.

The right cheek teeth are preserved in good condition, and their wear has not been excessive. P3 is peglike, and P4-M2 are triangular in shape. protocones are large and are attached to the paracones by a crest that varies from weak to strong. Protoconules are absent. The metacones and metaconules are equal in size to the paracones and are united to each other and to the protocones by crests. The mesostyles are low, but distinct, and are united to the paracones and metacones by crests. These crests and the external cingulum enclose the space on each side of the mesostyle, thus forming little pockets between the mesostyles and the neighboring cones. The anterior and posterior cingula on M1 and M2 are low, but distinct. On P4 the anterior cingulum unites with the parastyle. The parastyle on P4 of No. 8342 is connected to the paracone by a crest, but no such connection is seen on the other specimen (Univ. Colorado Mus. No. 19852).

Hypocones are not developed on any of the teeth. The description given above applies to the fourth premolar and the first two molars. The third molar is similar to the first and second in having crests uniting the paracone to the protocone, anterior cingulum, and mesostyle, but otherwise it is somewhat modified. The metacone and metaconule are absent, and the posterior cingulum is expanded to form a large heel, thus making a basin between the posterior cingulum and the protoloph. Faint traces of the valley that divided the posterior cingulum from the metaloph are still visible. In structure of

EXPLANATION OF PLATE 2	
A-Prosciurus relictus (COPE). No. 8333. Dorsal, lateral, ventral, and anterior views of anterior part of skull. Appro	PAGE OXI-
mately × 2.9	52
B—Cedromus? sp. No. 8342. Dorsal, lateral, ventral, and posterior views of the posterior part of the skull. Appr	oxi-
mately × 1.8	. 59
C—Cedromus? sp. No. 8342. Occlusal view of right P3-M3. Approximately × 5.5	60

PLATE 2 VERTEBRATA, ARTICLE 4 В

the talon, the tooth differs radically from the upper third molar of *Prosciurus*. In *Prosciurus*, the posteriorly placed metacone forms the heel but retains a weak connection with a reduced metaconule, which, in turn, retains its connection with the protocone. In addition, the lophlike crests from the mesostyles that extend into the basins in the molars of *Prosciurus* unite in the third molar with the metaconule or the protocone. With the exception of the crest from the mesostyle, both methods of developing the heel are seen in present day sciurids. In Oligocene times heel structure could have well been more stable, and only in more recent times did the sciurids simulate the heel structure pattern of the Prosciurinae.

Woon (1937, p. 163) has described the posterior part of a skull (AMNH No. 1429) which he thought might be that of a prosciurine. This skull differs from No. 8342 in having the palate wider, but this may be caused, in part, by crushing in the American Museum skull. The auditory bullae are narrower transversely at the anterior end, and the notch is not so wide or deep. Posteriorly, where the bullae of No. 8342 are compressed, those of the American Museum skull are wider. The teeth are different, and this skull probably does not belong to the genus Cedromus or Prosciurus but may belong to the genus Pelycomys. The straight basicranial axis of AMNH No. 1429 lends weight to the opinion that it probably belongs to the Prosciurinae rather than the Sciuridae.

The skull of No. 8342 differs from those of primitive rodents in having a bent basicranial-facial axis.

The broad palate and large heel of M<sup>3</sup> may be duplicated in the paramyine group. Whether or not the arrangement of the bones around the sphenopalatine foramen is a primitive feature remains to be decided.

No. 8342 differs from Prosciurus relictus in having a wider palate and more sciurid-like zygomatic arch. Nothing, however, is definitely known about the basicranial-facial axis in *Prosciurus*. If the skull discussed by Wood is a prosciurine, then the prosciurids do not have a bent axis comparable to that in No. 8342. The differences in the teeth are striking. The teeth of Nos. 8342 and 19852 (Univ. Colorado Mus.) differ from those of Prosciurus relictus and P. vetustus in having crests connecting the mesostyles with the paracones and metacones, in not having crests extending into the basins of the teeth from the mesostyles, in not having hypocones, in having better developed cingula, in not having protoconules, and in having a different type of heel in  $M^3$ .

Woon's description (1937, pp. 164, 171) of *Prosciurus* sp. (Princeton Univ. Mus. Nos. 14241-14242) seems to agree well with the tooth pattern of No. 8342.

The skull of No. 8342 resembles that of *Sciurus* in general shape and in having a bent basicranial-facial axis, a wide palate, a well-developed heel on M<sup>3</sup>, and ossified and strongly attached auditory bullae.

Wilson considered the following possible relationships for *Cedromus wardi*: (1) it is a paramyine; (2) it is a prosciurid evolving in the direc-

TABLE 10.—Summarization of the characters of Prosciurus, Pelycomys, and Cedromus

V.	Prosciurus	Pelycomys	Cedromus			
Lower teeth:						
Incisor width	Relatively wide	Most compressed	Medium			
Trigonids	Narrow	Wide	Wide			
Trigonids Metastylids	Free	United to metaconid	United to metaconid			
Metaconid	Compressed antero- posteriorly	Not compressed	Not compressed			
Metalophulid II	Short on all molars	Weak, but complete on M <sub>1</sub> -M <sub>2</sub> <sup>a</sup>	Short on all molars			
Entoconids	Large	Large	Small			
Hypoconids, M <sub>1</sub> -M <sub>2</sub>	Large	Large	Small			
Hypoconid, M <sub>3</sub>	Large	Large	Large			
Posterolophids	Separated from entoconid by notch	Separated from entoconid by weak notch	United to entoconid			
Hypolophulid	Present, and tends to unite with postero- lophid	Present, and united to ectolophid only*	Crest from entoconid turns back in basin			
Upper teeth:						
Anterior cingula	Present	Present	Strong			
Posterior cingula	Weak	Weak	Moderate			
Parastyle on molars	Present	Present	Absent			
Hypocones		Present	Absent			
Mesostyle	Crost into basin	Crest into basin				
			Crests to paracone and metacone			
Third molar	Mesostyle and metacone united to metaconule by crests; metacone forms heel	P	Mesostyle united to para cone; metacone lost; hee formed by posteroloph			

Absent in M<sub>3</sub> of Cedar Creek form, showing the extent of basining of M<sub>3</sub> in this species.

tion of a true squirrel type; and (3) it is a very primitive squirrel. He favored the first alternative stating (1949, p. 32) "Cedromus is placed in the Ischyromyidae, and tentatively in the Paramyinae because it cannot be distinguished really from members of this group, one of which is now known from a comparable geologic age; it is not like typical Prosciurus; and any other assignment is too speculative." Cedromus is not like Prosciurus or any related genus, and it is like the paramyines. The new material strongly suggests, however, that primitive sciurids existed in the middle Oligocene, and quite possibly Cedromus is such a sciurid, with many of its features reflecting the paramyine ancestry of the sciurids. This suggestion is supported by two facts neither of which is proof of relationship: (1) nothing in the tooth pattern or jaw structure of Cedromus prevents it from being ancestral to the typical sciurids; (2) primitive sciurids of the size of Cedromus are present in the middle Oligocene, represented by upper teeth and skull fragments. Or, to put this in another way-since lower teeth are present which are sciurid-like but not prosciurinelike, and upper teeth and skull fragments are also present which are here assigned to the sciurids, it is only natural to consider an association of the specimens.

That the skull (No. 8342), at least, represents a new species is more than likely, since there is a considerable stratigraphic difference between the level at which the type of Cedromus wardi was found and the level of this specimen. The specimens may also differ in size. These differences are not diagnostic, however, and do not justify a new name in

this case.

Table 10 summarizes the characters of three genera of structurally similar rodents from northeastern Colorado and strongly suggests that Prosciurus and Pelycomys are more closely related to each other, structurally at least, than to Cedromus.

A comparison of the skulls of Prosciurus and Cedromus? is not necessary here, as reference to the description of the Cedromus? skull will show that they are different.

#### FAMILY GEOMYIDAE GILL?, 1872

#### Diplolophus sp.

Referred specimen.—Cedar Creek member (middle): No. 9830; upper M1; SE¼ sec. 3, T. 11 N., R. 54 W., Logan

This lone tooth, the only representative of this genus from northeastern Colorado, is similar in pattern and occlusal wear to the M1 of No. 9-5-7-36 S. P. of the Nebraska State Museum, which Bar-BOUR & STOUT (1939, pp. 30-32, fig. 14E) referred to Diplolophus insolens TROXELL. However, the tooth is smaller and relatively narrower transversely (antero-posterior length 2.55 mm., and transverse width 2.20 mm. at occlusal surface) than the specimens referred to by Barbour & Stout.

# FAMILY HETEROMYIDAE ALLEN & CHAPMAN, 1893

#### Heliscomys vetus Cope

Heliscomys vetus Cope, 1873c, p. 3.

Type.—AMNH No. 5461; Cedar Creek beds of northeastern Colorado (fide Wood, A. E., 1937).

Referred specimens.—Cedar Creek member (lower): No. Referred specimens.—Cedar Creek member (lower): No. 8214; left jaw with M<sub>1</sub>. No. 8215; left jaw with P<sub>4</sub>-M<sub>1</sub>. No. 8216; right jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8217; left jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8984; right jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8985; left jaw with P<sub>4</sub>-M<sub>3</sub>. No. 8986; left jaw with M<sub>1</sub>-M<sub>3</sub>. No. 8987; right jaw with M<sub>1</sub>-M<sub>2</sub>. No. 8988; right jaw with P<sub>4</sub>-M<sub>1</sub>. No. 8989; left jaw with P<sub>4</sub>-M<sub>1</sub>. No. 8990; right jaw fragment with P<sub>4</sub>. No. 8991; right jaw fragment with P<sub>4</sub>. No. 8991; right jaw fragment with P<sub>4</sub>-M<sub>3</sub>. No. 8994; left maxillary fragment with P<sup>4</sup>-M<sup>3</sup>. No. 8994; left maxillary fragment with P<sup>4</sup>-M<sup>1</sup>. No. 8996; left maxillary fragment with P<sup>4</sup>-M<sup>1</sup>. No. 8996; left maxillary fragment with P<sup>4</sup>-M<sup>1</sup>. Above 17 specimens from SW<sup>4</sup> sec. 12, T. 11 N., R. 54 W., Logan County. California Inst. Tech. (uncatalogued); right P<sub>4</sub>-M<sub>3</sub>, right P<sub>4</sub>-M<sub>2</sub>, right M<sub>1</sub>, left P<sub>4</sub>-M<sub>2</sub>, left I, P<sub>4</sub>-M<sub>2</sub>. Above five specimens from SE<sup>4</sup> sec. 17, T. 11 N., R. 65 W., Weld County.

The specimens from Logan County were collected at one level and within a few feet of each other. The specimens in the California Institute of Technology were collected by Mr. James Mellinger of Longmont, Colorado, from a small remnant of channel deposit in sec. 17, T. 11 N., R. 65 W., of Weld County, which has been the source of a considerable microfauna. These specimens undoubtedly represent one species, and they present an unusual opportunity to study the variations present in the teeth.

Heretofore no upper teeth have been known that could be referred to Heliscomys vetus. The specimens described here are referred to this species because of their small size and because they were found in association (not occlusal) with lower jaws

referred to this species.

The upper premolar is as variable as the lower premolar of the species. The basic pattern is one with an anterior cusp, and three posterior cusps forming a metaloph, of which the metacone and hypocone are nearly equal in size and the entostyle (or lingual cusp) is reduced. No cingula connect any of the cusps, and the valleys are deep, especially between the anterior cusp and the other three cusps. Only one specimen, No. 8995, has a small cuspule on the antero-external base of the anterior cusp. The entostyle is the most variable of the cusps, being prominent in the largest premolar and reduced almost to extinction on the two smallest premolars. In No. 8996 the entostyle is reduced, less than in the two smaller specimens but more than in the largest, and the metacone is unusually large. However, in the smallest specimen the hypocone is largest. There seems to be a definite correlation between the size of the premolar and the amount of reduction of the entostyle.

All of the cusps on M1, including the internal cingular cusp, are high, prominent, and separated by deep valleys. The internal cingular cusp is

opposite the transverse median valley. A cingulum passes across the face of the tooth and the inner side from the paracone to the internal cingular cusp. No other cingula are present. The paracone and metacone are set slightly in advance of the protocone and hypocone.

M<sup>2</sup> is similar to M<sup>1</sup> in pattern, except that the paracone and metacone are not advanced forward

in relation to the other cusps.

M<sup>3</sup> has the metacone and hypocone reduced, but the paracone and internal cingular cusp are large and well developed. Wear on the only M3 in the group prevents determining the size and development of the protocone. Apparently a cingulum connects the paracone and internal cingular cusp on this tooth.

In the lower fourth premolar the entoconid is rather constant in size and shape. The hypoconid is generally equal in size to the entoconid but may be larger. The hypoconulid, present on the posterior edge of the tooth, varies in length and in width across the rear of the tooth. Important and significant variations take place in the anterior part of the tooth. The principal cusp in this part is the metaconid which is always smaller than the hypoconid and entoconid. The protoconid is present in some teeth and lies on the antero-external border of the tooth. The following variations occur:

(1) Protoconid cone-shaped, and almost as large as metaconid; pattern almost symmetrical. Example: California Inst. Tech. specimen.

(2) Protoconid obliquely compressed and much smaller than metaconid; tooth pattern asymmetrical. Examples: Nos. 8215, 8217, 8992, and two California Inst. Tech. specimens.

(3) Metaconid reduced to size of small proto-

conid. Example: No. 8990.

(4) Metaconid weak and small; protoconid absent; hypoconid larger than entoconid and extended forward into area occupied by protoconid as if seemingly fused with that cusp. Examples: Nos. 8216, 8988, 8989, 8991, and California Inst. Tech. specimen.

The pattern of the first and second lower molars is that of four well-developed primary cusps more or less bordered on three sides by low cingula which develop cusps. The primary cusps are separate from each other, but, with wear, they tend to form lophids. Of the two cingular cusps, the protostylid is larger than the hypostylid, and both are as high as the protoconid and hypoconid cusps. Each stylid is placed slightly posterior to its corresponding primary cusp. The antero-external part of the cingulum is generally well developed and forms a cusp, but sometimes it is weak and reduced. In most of the teeth, the anterior cingulum is united to the antero-internal angle of the protoconid by a crest. Beyond this crest the cingulum is weak and normally fades out on the face of the metaconid. The union of the antero-external part of the cingulum to the protostylid, where both structures are

strong, may be broken by a well-developed notch; or, where the cingulum is weak, it may unite to the stylid without the presence of a notch. The notch between the stylids varies in depth. Posterior to the hypostylid the cingulum varies from strong to weak, in some specimens extending across to the posterior face of the entoconid and in others fading out on the posterior face of the hypoconid. A cusp of variable strength develops in the cingulum opposite the opening of the valley between the entoconid and hypoconid. In some specimens it is the strongest part of the cingulum. Approximately two of every three teeth have strong antero-external cingula, anterior cingula united to protoconids, protostylids and hypostylids divided by a deep notch, and weak posterior cingula. In spite of the variations mentioned, the basic pattern of the teeth remains unchanged, being rather close to that of Heliscomys hatcheri.

The third lower molar is composed of four welldeveloped primary cusps, of which the hypoconid and entoconid show slight reduction in size. The protoconid and metaconid are united by an anterior crest. The anterior cingulum is weak on the face of the metaconid, absent at the mid-line of the anterior surface of the tooth, and stronger on the anterior and external faces of the protoconid. Incipient cuspules are formed in positions corresponding to the stylids of the first and second molars. Posteriorly, the cingulum disappears, but a small cuspule is present on the postero-internal face of the entoconid of one specimen. The above description of M<sub>3</sub> represents the optimum condition seen in these specimens (especially No. 8217, which is unworn), and variations consist of weaker development of the structures.

In shape the lower molars generally have the antero-posterior length equal to the transverse width, but they may vary in having the anteroposterior length greater in the first molar, the transverse width greater in the second molar, and either the antero-posterior length or transverse width

greater in the third molar (Table 11).

This group of specimens is significant because the range of variation in the teeth encompasses most of the characters used to describe the species of Heliscomys. At the same time, the range of variation in the molars is small enough to necessitate keeping the group in one species that exhibits a high degree of variability in the premolars. At present I would doubt the validity of any species based upon differences in the premolar or small differences in the proportions of the molars, unless these differences can be shown by large samples to occur constantly or can be shown to occur with other differences such as geological age, actual size, or relative size among teeth.

Because the specimens represent, at the very most, no more than two populations of the same species, they present evidence on the evolution of the lower premolar in the primitive heteromyids. As may be seen, the simplest and most complex premolar patterns are present at each of the two localities and are found in both the smaller and larger specimens. A similar range of variation in Heliscomys hatcheri was found by A. E. Wood (1939, p. 555). Different opinions have been advanced as to whether the premolar is losing or gaining cusps. Woop (1937, p. 211) suggested that in the genus a cusp had been added to the three primary cusps but commented upon the difficulties involved in such a hypothesis in homologizing the cusps with those of other rodents. Later (1939, p. 560) he thought that the specimens of Heliscomys hatcheri examined by him suggested that the threecusped condition was the result of degeneration but did not think the evidence was conclusive. Mc-Grew (1941b) considered the three-cusped condition to be primitive. Wilson (1949b, p. 115) favored the view that the primitive pattern was one of four cusps and that Heliscomys was undergoing reduction of the premolar. The Miocene species, Heliscomys woodi, with its reduced three-cusped premolar was cited as an example in support of this view. The specimens from northeastern Colorado support the hypothesis of a four-cusped P4 in the primitive forms. The fact that the metaconid is small, as in the premolar of No. 8216, argues against its representing a primitive stage in the Heliscomys line, inasmuch as an ancestral rodent with a premolar pattern entirely unlike any known early rodent pattern would be required to supply the pattern, or else an extraordinary reversal of trend took place. On the other hand, the premolar of the California Institute of Technology specimen, which has the protoconid cone shaped, is closer to the primitive rodent tooth pattern. Although the sample is small, it is tempting to think that some of the specimens (those with three large cusps and a small protoconid) represent the norm for the group, while the remainder represent the less progressive and the more progressive forms. This hypothesis is a more logical explanation of the premolar evolution in Heliscomys than the alternate hypothesis that would explain the extremes of this population as separate phylogenetic lines, which were ancestral respectively to Heliscomys woodi and Proheteromys. From a purely structural point of view, however, the less progressive, four-cusped specimens of Heliscomys do show a closer relationship to Proheteromys because they are closer to the premolar pattern of the ancestral rodent that gave rise to Proheteromys and Heliscomys.

Heliscomys has often been referred to as the ancestor of the heteromyids. In my opinion this genus is an aberrant branch of the *Proheteromys* stock that trended toward reduction of the premolars.

# Heliscomys tenuiceps Galbreath

Heliscomys tenuiceps Galbreath, 1948, p. 289.

Type.—Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist. No. 7702; Cedar Creek member (middle), White River formation, SE¼ sec. 3, T. 11 N., R. 54 W., Logan County, Colorado.

Table 11.—Measurements (in mm.) of Heliscomys vetus\*

							No	. 8993		N	o. 8994	4	N	lo. 899	5	N	lo. 899	96
Crown length of P4-M3		4 4 4 4						2.85										
Alveolar length of P4-M3							90	3.10						22.01				
P4, antero-posterior length								0.75			0.51			0.81			0.75	
P4, transverse width	Ya Trai	214/202	72/14/12/13/14	007/2020	21212121			0.78			0.63			0.96			0.90	
M1, antero-posterior length								0.84			0.81			0.93			0.87	
M <sup>1</sup> , transverse width								1.05			0.84							
M², transverse width	****		50.55		3.000									1.17			1.14	
M <sup>2</sup> , antero-posterior length	55.53	****		or early	3335	5555	200	0.72			0.72			1000			1000	
M <sup>2</sup> , transverse width	4.4.4.3		*25.5557		313333	00000		0.92			0.81			* * * * *				
M <sup>3</sup> , antero-posterior length	*0×(4)+	*: *: *: *:	+ + + + +					0.54			0.0000							
M <sup>3</sup> , transverse width	x = 0.7e						. (	0.69			# (# C# (A			****				
		No. 8215	No. 8216		No. 8984	No. 8985	No. 8986	No. 8987	No. 8988	No. 8989	No. 8990	No. 8991	No.		Califor Fechno	nia In	stitute	of
		TELET.	2000	The second											_			
Crown length of P <sub>4</sub> -M <sub>8</sub>	Service III	ACRES NO.	*****	Caraba Servi		600.000	0.33						0.45	2.89				57.5
P4, antero-posterior length		0.51	0.57	0.60	0.51	0.48			0.51	0.48	0.45	0.45	0.48		0.57	0.45		0.5
P4. transverse width		0.57	0.66	0.63	0.60		2227			0.54	0.48	0.51		0.57				0.6
M <sub>1</sub> , antero-posterior length	0.87	0.78	0.87	0.84	0.87	0.90	0.78	0.90	0.84	0.87	****	K 1000	0.84	0.87	0.84	0.87	0.84	
M1, transverse width of anterior	0.00	0.70	0.00	0.01	0.04		0.70	004	0.01	0.04							122	
lophid	0.90	0.78	0.90	0.81	0.84	1000	0.78	0.84	0.01	0.87	2.0.00		0.87	0.84	0.84	0.84	0.81	0.8
lophid	0.84	0.78	0.84	0.81	0.81		0.75	0.78	0.84	0.78			0.00	0.01	0.84	0.01	0.70	
Ma, antero-posterior length				0.81	0.75	0.75	0.72	0.84	0.04	0.76			0.90	0.78	0.87	0.81		0.8
M <sub>2</sub> , transverse width of anterior														0.10	0.01	0.01	1111	U.01
lophid			0.87	0.81	0.87		0.81	0.84						0.84	0.87	0.84		0.8
Ma. transverse width of posterior																		
lophid	1000		0.75	0.78	0.84		0.72	0.75	11.00	4.1.4.4					0.87	0.75		0.7
Ms. antero-posterior length	202.20	5755	0.66	0.69	0.72	0.63	0.63	5555	27.77	45,515.5	37.55		F:4000	0.66	*:51*15		****	
Ma, transverse width of anterior			0.70	0.66	0.66		0.60											
lophid	1.5.0		0.72	0.00	0.00	* 7 7 9	0.03	* * * *		****				0.63	0.000		****	
Ma, transverse width of posterior lophid			0.57	0.57	0.60		0.54							0.54				
Depth of ramus at P.			0.01	0.01	2.50		0.04		2.36	CARROLL .		Dece 213	9.40	0.04		* * * *	****	
septim or ramino as a ferressistance	12.75.77			AUTORIA.	Land	01.11.112	111.000	ARREAGE.	- 34 AVX.	7.5.15.17.13					2.71.00	***		

a. These measurements were made by grid with a length per unit of 0.03 mm.

In the original description the term sphenofrontal foramen was applied to a foramen in the orbital wall. Further study of this area suggests that this foramen is the anterior ethmoid foramen. It is possible that a fracture line was misinterpreted as a suture; if so, the alisphenoid bone did not extend so far forward as was described. Although either interpretation may be made, it is more in keeping with related groups to consider the foramen as the anterior ethmoid.

#### Proheteromys? sp.

Referred specimen.—Cedar Creek member (lower): Chicago Nat. Hist. Mus. No. PM381; anterior part of right jaw with I, P<sub>4</sub>-M<sub>1</sub>; SE¼ sec. 17, T. 11 N., R. 65 W., Weld County.

This specimen is recorded in the Chicago Natural History Museum records as coming from the "Mellinger locality" which is the level and locality cited above (see also Patterson & McGrew, 1937, and my discussion of Heliscomys vetus). The evolutionary stage represented by this specimen and the presence of Miocene deposits channeled into the Cedar Creek member at this locality make the exact location and level of this specimen of extreme importance. Neither the matrix nor state of preservation suggests that the specimen came from any bed other than the "Mellinger locality."

Differences from Heliscomys vetus are seen in the greater antero-posterior length of the teeth (Table 12); presence of four well-developed cusps corresponding to the three large cusps and small protoconid on the P<sub>4</sub> of Heliscomys; presence of a small anteroconid, and behind it, a second larger "anteroconid" that lies between the metaconid and protoconid on P<sub>4</sub>; and oblique elongation of the principal cusps of the molars which join to form lophids and an incipient H pattern. Except for a nearer correspondence in size, the specimen differs in the same ways from those of Heliscomys hatcheri.

Characters used to distinguish No. PM381 from Heliscomys are: larger jaw and incisor; longer tooth row; differences in the premolar pattern; changes in the prominence and development of the cingulum; and differences in the molar occlusal pattern. The tentative assignment of this specimen to Proheteromys is made on the basis of similarity of the characters mentioned to those in specimens of Proheteromys floridanus, P. thorpei, and P. nebraskensis. The four well-developed cusps and

TABLE 12.—Measurements (in mm.) of Proheteromys? sp.

															No.	PM381
I, antero-posterior length .				4		-	35					្		 	040	1.15
I, transverse width		10	i.	1			3			a	1		्र		2	0.67
P4. antero-posterior length																0.69
Pa. transverse width																0.66
																0.96
M <sub>1</sub> , transverse width	٠.				٠.			c.v			v.			 ٠.		0.87
Depth of ramus at P4			0	0					5			en Ro			147	3.30

a. Chicago Natural History Museum.

anteroconid of P<sub>4</sub> and the reduced cingula and obliquely directed cusps of the molars are points in common between No. PM381 and specimens of *Proheteromys*, especially *P. floridanus*. A difference which may prove to be phylogenetically significant is the well-developed anteroconids, a feature which is not so prominent in *Proheteromys*.

A conclusion drawn from the study of the lower jaws of *Heliscomys vetus* is that variation in the cusp pattern of the premolar and that minor differences in the proportions of the molar teeth should not be used to distinguish species in the genus. Inasmuch as the Chicago Museum specimen is close in size to specimens of *Heliscomys*, considerable attention was devoted to determining whether it could be an aberrant individual in a population of *H. vetus* or referable to *H. hatcheri*. For the reasons cited above, these possibilities do not seem likely.

If this specimen came from the exact locality that yielded the *Heliscomys vetus* jaws, then it represents the earliest known record of the *Proheteromys* type of heteromyid and shows the close relationship of this genus to *Heliscomys*.

# FAMILY CASTORIDAE GRAY, 1821

# Agnotocastor coloradensis Wilson

Figure 20

Agnotocastor coloradensis Wilson, 1949, p. 32.

Type.—Univ. Colorado Mus. No. 19809; Cedar Creek member; center of W½ sec. 21, T. 11 N., R. 53 W., Logan County, Colorado.

Referred specimens.—Cedar Creek member (lower): No. 8226; maxillaries with left P<sup>4</sup>-M<sup>1</sup> and right M<sup>1</sup>-M<sup>2</sup>. No. 8227; maxillary with right P<sup>3</sup>-M<sup>2</sup>. No. 8228; anterior part of crushed skull with right P<sup>4</sup>-M<sup>3</sup> and left P<sup>4</sup>-M<sup>3</sup>. No. 8229; maxillary with right P<sup>3</sup>-M<sup>2</sup>, right jaw with P<sub>4</sub>-M<sub>1</sub>, and right jaw with M<sub>1</sub>-M<sub>2</sub> (associated). No. 8230; right jaw fragment with P<sub>4</sub>-M<sub>2</sub>, and fragment of incisor. No. 8231; right jaw fragment with P<sub>4</sub>-M<sub>2</sub>. No. 8232; frontal bones of skull. No. 8233; left jaw with M<sub>1</sub>-M<sub>2</sub>. No. 8234; fragment of left maxillary with P<sup>4</sup>-M<sup>1</sup>, and right jaw with M<sub>1</sub>. All specimens from bed of olive-colored silt at type locality.

Additional information concerning this species is contributed by these specimens. No. 8228, a skull fragment, is badly damaged, but enough is preserved to show that the rostrum is relatively long as in Agnotocastor praetereadens Stirton. The inclination of the zygomatic plate is similar in the two species, but the posterior end of the zygomatic root of A. coloradensis has its origin over the anterior part of P4. The anterior end of the infraorbital canal is pushed forward on the rostrum and is bordered by a heavy tuberosity as in A. praetereadens. Except for the place of origin of the posterior part of the zygomatic root, the preserved part of the skull is similar to that of A. praetereadens and totally unlike that of Eutypomys thomsoni MAT-THEW.

The lower jaws exhibit the same stubbiness and great depth shown in the type specimen.

The specific characters of the lower teeth, given by Wilson (1949, p. 32), are apparent in the material here reported upon. The fact that none of the incisors are brightly colored lends support to this character cited by Wilson. It should be kept in mind, however, that all of the specimens are from the same locality and level as the type specimen and that, consequently, the dull color of the incisors may reflect only the local conditions of preservation.

The occlusal patterns for the specimens are presented diagrammatically in Figure 20. A certain arbitrary arrangement of the individual tooth rows from youngest to oldest was necessary inasmuch as there are differences in pattern and in rate of eruption and wear of the individual teeth. For example, the entoconid of  $M_1$  of No. 8229 represents a younger individual age than does the entoconid on the  $M_1$  of No. 8230. Yet the  $M_2$  of No. 8230 is in an older stage of wear than that of No. 8230. Such individual variations are to be expected, and a certain amount of subjective judgment in such matters must be used in comparing the specimens.



Figure 20.—Agnotocastor coloradensis Wilson. Left column: occlusal patterns of upper teeth arranged from youngest to oldest in descending order. Right column: occlusal patterns of lower teeth arranged from youngest to oldest in descending order. Occlusal patterns of upper teeth of Nos. 8234 and 19809 reversed. Thickness of lines shows approximate thickness of enamel bands. With exception of M<sub>1</sub> in No. 8230, and P<sup>3</sup> in No. 8227, no reconstruction (dotted lines) of damaged enamel has been attempted. Approximately × 4.

TABLE 13.-Measurements (in mm.) of Agnotocastor coloradensis

	No. 8226	No. 8227	No. 8228	No. 8229	No. 8234	No. 8230	No. 8231	No. 8233
Crown length of P4-M3	hi sustana	(8)8)8(8)	15.0+	4:4:4:4	24.83			
I. transverse width	or arrangement	* * (* * )	4.4	F-F-5-2	(5) (5) (5) (5)	***		3.5 (5.5.5)
P <sup>3</sup> , antero-posterior length	A 31 T 2	1.1		1.1	******		* (* (* (* )	35.505.5
P <sup>3</sup> , transverse width	1.0000	1.6	24.41414	1.7	9.4.6.6	0.0000	10.000	)# (@),# (W)
P4, antero-posterior length		4.3	4 4 4 4	4.2	4.0	2404969	****	38363636
P4, transverse width	0.20000	5.5	5.0	5.2	5.1			2000
Mi, antero-posterior length	3.4	3.4	3.6	3.5	3.3	352.22	22.472	Water
M1. fransverse width	50		4.9	4.7	5.2			
antero-posterior length	3.3	3.3	3.5	3.6	14.45.4 (4.5	20.525.6		
M <sup>2</sup> , transverse width	4.6	4.8	4.9	4.5	* * * *			
M <sup>3</sup> , antero-posterior length	F T T F	******	3.1	# (# (# )#	* (YS C.)			
13, transverse width		# T 4 D 1	4.0	4.4.4.4	10000	2000		*****
transverse width		99949	43.44		***	4.0		4.0
4, antero-posterior length		9999		3.7		3.9	4.5	
4, transverse width	20000	23.50	2000	4.1	201201	4.3	2020213	2000
M <sub>1</sub> , antero-posterior length	2000		4.244	3.6	3.7	3.7	3.8	3.6
1, transverse width	5.000.0	8272		4.2	4.2	4.3		4.5
12, antero-posterior length	5:1000			3.7	*****	3.8	3.7	
M <sub>2</sub> , transverse width		(0.00 to 10.00 to 10.	25.5.2.8 200.6.8	4.4		4.1		200
Depth of jaw below middle of P4	5.0.7.9				11111		1.1.1.1	15.0

The terminology used in this discussion is the same as that used by Wilson (1949), but my interpretation of the homology of the mesolophid in the lower teeth of this species differs from that of WILSON. WILSON uses the term mesolophid for the anterior arm connecting the entoconid and ectolophid. When observed on the younger individuals of the species, this structure seems not to be a true mesolophid, but instead a hypolophulid I. If this be true, the M1 and M2 of No. 8229 suggest that an incipient mesolophid in some teeth meets the hypolophulid and forms the anterior arm. The plasticity of the structures in the area surrounding the mesolophid is demonstrated by No. 8234 which has the metastylid developed to the point where it unites with the mesolophid. This variation suggests an extreme interpretation of the structures that is reminiscent of the condition seen in Eutypomys. Perhaps the metastylid cusp (or cusps) and the mesolophid are remnants of a complete mesolophid, which has broken up, with the various parts be-coming associated with the metaconid and ento-

Like Agnotocastor praetereadens, the upper teeth of A. coloradensis are elongate transversely (Table 13), and the incisors are convex on their anterior surfaces, but the pattern of the cheek teeth is much more complex and primitive (unless wear has completely removed all trace of the original complexities in the pattern of A. praetereadens). Nor do the teeth of A. coloradensis have the shape or crenulate complexity of those of Eutypomys. The homologies of the posterior parts of the upper teeth seem to be clear, but the crests of the anterior parts are more difficult to homologize with parts of the primitive rodent tooth. For the parts in question, the terms anterior cingulum, protolophule, and mesoloph are used here. Although it might be safer and less confusing to use the terms anterior

cingulum, protolophule I, and protolophule II, the use of the term protolophule II would imply that the mesoloph was absent in the upper teeth, an implication that is contrary to the evidence at present. Some of the features of the type specimen, which were not readily decipherable when Wilson described this species, are clarified by the present material. The complexity noted by Wilson (1949, p. 33, last paragraph) in the anterior part of the molars is explained by the structures seen in the molars of the young specimen, No. 8229, which seem to me to be the anterior cingulum, metalophulid I, and metalophulid II. Wilson (p. 34) was uncertain about the completeness of the "hypolophid" in unworn molars but suggested that it resembled the hypolophid of the premolar in this respect. This suggestion is correct, but a union seems to be rapidly formed between the "hypo-Wilson suggested lophid" and the ectolophid. what the diagnostic features might be of the immediately ancestral beaver pattern, as inferred from A. coloradensis. Our additional material permits certain minor changes in and additions to Wilson's statements (p. 34): "(1) early union of the lingual end of the posterolophid with the entoconid, if these were ever separate [These structures were separate and do unite early in life.]; (2) a welldeveloped mesolophid in the molars, uniting with the entoconid upon wear [This structure has been discussed, and I think that it might be a hypolophulid I uniting with the ectolophid or poorly developed mesolophid.]; (3) relatively incomplete hypolophid [This structure is incomplete, regardless of its identification as a hypolophid or hypolophulid II.]; (4) strong metastylid (or mesostylid) structures [The multiplicity of cusps seen in some of the specimens suggests that both metastylid and mesostylid cusps may be involved or that one or the other may be dominant as an individual variation.]; (5) well developed metalophulid II [This is true.]." Wilson commented upon the incomplete ectolophid in *Eutypomys* which was inconsistent with his comparison of *A. coloradensis* with *Eutypomys*. P<sub>4</sub> of No. 8230 suggests that this separation did exist in *A. coloradensis* and strengthens the case for close association of the eutypomyids and castorids.

Although these new specimens yield more information than has heretofore been available about the primitive castorid tooth pattern, the situation remains as it was in the past: There is enough evidence to hazard tentative decisions about the homologies of the tooth structures and about the ancestral patterns, but not enough to satisfactorily clear up questionable points. The relationships of these teeth to those of the paramyine and sciuravine types are not clarified by the present specimens, inasmuch as they show affinities with both groups.

#### FAMILY CRICETIDAE ROCHEBRUNE, 1883

The treatment accorded the species in the family Cricetidae, especially Eumys obliquidens, E. elegans, and E. brachyodus, may seem unusual, but it is presented as an interpretation of the cricetid specimens (approximately 350 that had stratigraphic and areal position well enough known to be useful) from northeastern Colorado.

# Eumys obliquidens Wood

Eumys obliquidens Wood, A. E., 1937, p. 253.

 $Type.{\rm -\!AMNH}$  No. 5603; Cedar Creek middle Oligocene beds of Colorado.

Referred specimens. — Cedar Creek member (lower): Nos. 8430 and 8435; right and left lower jaws with M<sub>1</sub>-M<sub>3</sub>; NE¼ sec. 28, T. 11 N., R. 53 W., Logan County. No. 8484; left jaw with M<sub>1</sub>-M<sub>3</sub>; NE¼ sec. 8, T. 11 N., R. 54 W. (channel s. s.), Logan County. No. 8462; right jaw with M<sub>1</sub> and M<sub>3</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County.

#### Eumys elegans Leidy

Eumys elegans LEIDY, 1856, p. 90.

Referred specimens.—Cedar Creek member: No. 8429; anterior part of skull and left jaw in occlusion; SW¼ sec. 22, T. 11 N., R. 53 W., Logan County. No. 8475; anterior part of skull and right jaw in occlusion; SW¼ sec. 2, T. 11 N., R. 54 W., Logan Conuty. No. 8458; anterior part of skull; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County.

#### Eumys brachyodus Wood

Eumys brachyodus Wood, A. E., 1937, p. 252.

Referred specimens.—Vista member: Univ. Colorado Mus. No. 19870; left jaw with M<sub>1</sub>-M<sub>3</sub>; SE¼ sec. 8, T. 11 N., R. 53 W., Logan County. No. 8427; left jaw with M<sub>2</sub>; SE¼ sec. 8, T. 11 N., R. 53 W., Logan County. No. 8979; left jaw with M<sub>1</sub>; NE¼ sec. 17, T. 11 N., R. 53 W., Logan County.

The specimens assigned to Eumys obliquidens are like the type in that they have the mesolophid of  $M_1$  longer or as long as the posterior arm of the protoconid and in that the posterior protoconid arms of  $M_2$  and  $M_3$  extend postero-mesiad to unite

with the entoconids on either or both teeth. Besides these, other specimens have either short mesolophids and turned-back protoconid arms or have the arm in one tooth turned back and the other forward. One specimen, No. 8452, from the middle of the Cedar Creek member, has a mesolophid on M, that reaches the internal surface of the tooth, but on both M<sub>2</sub> and M<sub>3</sub> the protoconid arms are united with the metaconids. These latter examples demonstrate that intergradation exists between this species and others. Another specimen, No. 8436, referred to this species and from the same level and locality as Nos. 8430 and 8435, deserves mention for an unusual construction. In this specimen the mesolophid is longer than the posterior protoconid arm on M1, equal in length to the posterior protoconid arm on M<sub>2</sub>, and absent on M<sub>3</sub> where the posterior protoconid arm turns back to join the entoconid. In size and pattern this specimen resembles Cricetodon nebraskensis Wood. However, to regard the long mesolophids of M<sub>1</sub> and M<sub>2</sub> as a valid generic character seems unreasonable, especially when the specimen concerned occurs within a population which has considerable variation in mesolophid length. So far as the specimens of E. obliquidens from northeastern Colorado are concerned, features common to the teeth listed, except No. 8452, are: (1) occurrence at the base of the Cedar Creek member, (2) tendency for the posterior arm of M<sub>2</sub> and M<sub>3</sub> to turn toward the entoconid, and (3) length of the mesolophid on M, variable but usually longer than the posterior protoconid arm. The evidence is negative in nature, but I have not found teeth in beds higher in the section that have the protoconid arm directed posteriorly.

Three specimens, Nos. 8429, 8458, and 8475, have been selected to represent the group of specimens that were collected from many points throughout most of the vertical and areal extent of the Cedar Creek member. All seem to be referable to *Eumys* elegans. These have characters of E. elegans or at least no characters that would allow reference to any other species. The skull fragment, No. 8458, differs from the other skull fragments assigned to E. elegans. The snout is broader and deeper but not longer, thus giving the appearance of shortness. The nasal bones are broader with the lateral borders more sinuous. The teeth are shorter (Table 14). Also, several small jaws with small teeth are present in the deposits, but the occlusal patterns show no constant differences, and they could well be treated as small individual variants of E. elegans. Analysis of the size range of large groups of lower teeth shows the possible presence (as part of a bimodal curve) of this "species" in the *Eumys* population.

A. E. Woop (1937, p. 252) listed *Eumys brachyodus* as occurring in Colorado, and probably in the Oreodon zone. The specimens listed above are the only ones seen by me that duplicate the description of this species in all particulars. In the Orellan

Table 14.—Measurements (in mm.) of Eumys obliquidens, Eumys elegans, and Eumys brachyodus

	E.	obliquide	าร		E. elegans		E.	brachyode	18
	No. 8430	No. 8435	No. 8484	No. 8429	No. 8458	No. 8475	No. 19870*	No. 8427	No. 8979
Crown length of M¹-M³	(SP2)2(C)	G2(2)(2)(2)	272/272	6.35	6.12	6.53	2/2/252	120276	
I, width		0.00	* * * *	1.42		1.26			0000
M1, antero-posterior length	22.55	11.55	17.77	2.70	2.64	2.79			
M <sup>1</sup> , transverse width	* * * *	111111	10011	1.90	1.80	1.81		* * * *	
M <sup>2</sup> , antero-posterior length	355.55	(*) * (*) *	1.7.5.4	1.92	1.86	1.98	17.55	****	4 4 4 4
M <sup>2</sup> , transverse width	****		*****	1.86	1.86	1.79	F 9 3 9 3	* * * *	
M <sup>3</sup> , antero-posterior length	200.00	4.4.4.4	2727272	1.56	1.47	1.65			E3E361#
M <sup>3</sup> , transverse width	2000	5.00	10000	1.89	1.74	1.69	2747272	1111	04000000
Crown length of M <sub>1</sub> -M <sub>3</sub>	6.91	6.50	7.05	4.60	200	6.90	7.02		
, width	0.01	1.58		1.26		2.1.2.1		2222	
M <sub>1</sub> , antero-posterior length	2.46	2.37	2.52			2.19	2.34		2.31
M <sub>1</sub> , transverse width	1.74	1.79	1.78			1.66	1.99		1.75
of antere posterior length	2.16	2.04	2.19	2.16	52000	2.22	2.25	2.32	
M2, antero-posterior length	1.98	1.94	1.92	1.99	5.0000	1.91	2.28	2.12	33.53
M <sub>2</sub> , transverse width					500.505				2015/01/2
M <sub>3</sub> , antero-posterior length	2.25	2.01	2.25	2.04	P. S. P. S.	2.55	2.25	1.1.1.1	
M <sub>3</sub> , transverse width	1.89	1.82	1.81	1.89	6.000	1.84	2.08		9.50

a. University of Colorado Museum.

many specimens have one or more of the characters that distinguish E. brachyodus, but never all of them. The most common variants are those which show disappearance, with wear, of the inner half of the anterior cingulum on M<sub>2</sub>-M<sub>3</sub> without the presence of the other distinguishing characters, and those with one or more of the other distinguishing characters, but with a prominent cingulum. All of these specimens are referred to *E. elegans*. It is of interest that, of the specimens referred to *E. brachyodus* by Wood, all were from the upper Brule of Nebraska except those for which the level was uncertain, including the Colorado specimens. With the addition of our specimens from the Whitneyan, and in view of the lack of positively identified specimens from the Orellan, an argument for the Whitneyan age of E. brachyodus is strengthened. At the same time, identification of any Orellan specimens as E. brachyodus is rendered more unlikely.

The lower teeth of these three groups of specimens were arranged stratigraphically and analyzed on the basis of four characters which are presented

in tabular form (Table 15).

The variations and trend of changes in the crests uniting the anteroconid, protoconid, and metaconid present a complicated picture. Variation occurs (1) as differences in the strength of the crest connecting the protoconid and anteroconid and (2) in the presence, strength, and direction of the crest leading from the metaconid. The basic pattern of the earliest forms consists of a union of the protoconid to the anteroconid and of a free metaconid. The trend of change is toward the development of a crest from the metaconid that unites first with the crest leading from the protoconid to the anteroconid [as seen in the M, of Cricetodon nebraskensis figured by Woop (1937, fig. 68)], shifting subsequently to the anteroconid as is seen in E. brachyodus.

To make new species of the variants found in the

populations of Eumys obliquidens, E. elegans, and E. brachyodus (which is, in effect, limiting the range of variation in the species to the scope of the original diagnosis and to the description of the type specimen) is not acceptable in view of the intergradation that exists between the three groups. The simplest interpretation of the variations is that one species, Eumys elegans, represents a chronocline in which the mesolophids were shortened and finally lost, the posterior protoconid arms were turned forward and reduced, the connecting crests between the principal cusps and the anteroconid were developed, and the anterior cingula were reduced. In the lower beds specimens possessing certain combinations of these variable characters have been given the names Eumys obliquidens and Eumys In the same beds there are specimens which do not possess the complete suite of characters for either of the species but which intergrade with each. Higher in the beds there are not so many of the specimens with the variations that distinguish E. obliquidens, but variations appear that finally, when combined, distinguish Eumys brachyodus. Also present, of course, is the typical Eumys elegans. It might be argued that E. obliquidens and E. brachyodus represent extreme variations of E. elegans; but that these variants represent more than fortuituous combinations of characters that occur normally as variations in E. elegans seems indicated by the fact that one type of variant occurs at the bottom of the section and the other at the top. At least the order of occurrence suggests the trend of the changing characters. specimens may represent a form like E. obliquidens evolving into a form like E. brachyodus, with the transition stage being called E. elegans. I do not see any reason why there could not have been a gradual change of the genetic pattern that would yield E. elegans from an ancestor which looked more or less like E. obliquidens. Consequently, E. obliquidens represents that minor part of the

TABLE 15.—Summarization of the principal changes in the occlusal pattern of the lower teeth of Eumys

Stratigraphic position	Progressive shortening and loss of mesolophid on $M_1$	Tendency for posterior proto- conid arm to turn forward and reduce	Tendency for main cusps on M <sub>1</sub> to connect to antero- conid by crests	Reduction of anterior lingual cingulum on M <sub>1</sub>
Vista member	No mesolophid	United to metalophid and shortened in length	Both cusps united to anteroconid	Reduced
	Eum	ys brachyodus (s. s.); occurr	ence rare	
Cedar Creek member (upper part)	No mesolophid	United to metaconid	Protoconid united to anteroconid	Reduced
	Eu	mys elegans (s. l.); occurren	ce rare	
(middle part)	Frequently small or ab- sent, and rarely longer than posterior proto- conid arm	Tendency to turn for- ward and unite with metaconid	Same as below, but 33 percent have meta- conid crest united to protoconid crest	Variable in development
	Eum	s elegans (s. l.); occurrence	common	
(lower part)	Variable, but tends to be long, and frequently longer than posterior protoconid arm	More frequently turned to rear, or is variable on individual teeth	Most have protoconid united to the anteroconid, and metaconid free; 15 percent have arm from metaconid united to protoconid crest; uniting arm or arms are weaker and more frequently absent	Not generally reduced

Eumys elegans (s. l.); occurrence common

Eumys obliquidens (s. s.); occurrence—roughly one of every ten specimens has both the mesolophid longer than the posterior protoconid arm on  $M_1$ , and the arm turned back on  $M_2$ - $M_3$ 

E. elegans population which falls at the bottom or conservative part of the normal curve. Therefore, it would seem plausible that a minority of the specimens, those bearing brachyodus-like characters that were spreading genetically through the E. elegans population, would represent the progressive part of the population which finally found its expression in the late Oligocene as E. brachyodus. Until additional specimens of Eumys are found at lower stratigraphic levels, it will be impossible to verify the suggested relationship of E. elegans and E. obli-Unfortunately, eumyine specimens are quidens. not common in the upper part of the Cedar Creek member and the Vista member in northeastern Colorado; therefore, the record is equally faulty between E. elegans and E. brachyodus. The change from E. elegans to E. brachyodus may have been widespread and gradual. On the other hand, the characters discussed possibly were widespread, but were being swamped, and isolation at some geographic point permitted the combination of these to become established and to gain a foothold as a distinct species. The rarity of specimens in the upper Cedar Creek beds in northeastern Colorado and the abrupt appearance of E. brachyodus in the Whitneyan suggest that this is what may have happened. If the specimens of *E. elegans* reported from the Whitneyan of Nebraska are typical, support for this view is strengthened. On the other

hand, it could be argued, as it was for *E. obliquidens*, that the Whitneyan specimens of *E. elegans* represent the conservative part of the *E. brachyodus* population.

To arrange Eumys obliquidens and E. brachyodus as subspecies of Eumys elegans without information gained from studies of Eumys from other areas would be, in my opinion, an unwarranted and hasty action. Temporarily it seems best to continue using the three specific names for stratigraphic purposes in northeastern Colorado but it should be kept in mind that the groups are part of a chronocline.

# Eumys nr. E. exiguus Wood

Referred specimens.—Cedar Creek member: Nos. 8419-8420; left maxillaries with molars; SW% sec. 12, and SE% sec. 3, T. 11 N., R. 54 W., Logan County. Nos. 8421-8422; left lower jaws with molars; E% sec. 3, T. 11 N., R. 54 W., Logan County. Nos. 8423-8424; left lower jaws with molars; W% sec. 7, T. 11 N., R. 53 W., Logan County. No. 8426; right lower jaw with molars; SW% sec. 21, T. 11 N., R. 53 W., Logan County.

These specimens differ from the type specimen of *Eumys exiguus* only in their smaller size (Table 16). In our collection there are 12 specimens from the "middle" Brule of Sioux County, Nebraska, that nicely bridge the size gap between the Coloradan specimens and the type specimen from South Dakota. Whether or not this size cline represents

three successive stages leading from a small to a large form is not clearly evident. In northeastern Colorado the small specimens are found in the lower and middle part of the Cedar Creek member. It may be that they are older than the specimens from Nebraska and South Dakota. It seems improbable that the specimens from the three states represent geographic subspecies. To maintain such a view would mean rather close correlation of the beds of the three areas and narrow range of time

for existence of the species.

The northeastern Coloradan and the Nebraskan specimens, in general, show the following common features. The upper teeth tend to form a pattern in which the antero-posterior lophs are emphasized, with a consequent weakening of the transverse connections. This antero-posterior strengthening tends to be emphasized on the medial side of the tooth row. There are no connecting crests between the paracones and protocones, but a tendency toward this condition is apparent in some teeth. On M1 the protocone is united to the very large and well-developed anterocone by a weak crest, and on M<sup>2</sup> and M<sup>3</sup> the paracone and protocone arms unite before joining the anterior cingulum. The hypocone and metacone of M³ are reduced. The lingual and buccal anterior cingula on M2 are subequal in size, but the lingual cingulum on M3 is much re-The lower molars have, as rather consistently occurring characters, the mesoconids well developed; no mesolophids on M2 and M3; anteroconid of M, free or united to metaconid by an anterior metaconid arm; anterior metaconid and protoconid arms on M2 and M3 extended anteriorly to the anterior cingulum and never joined to one another; and posterior buccal cingula present on M<sub>1</sub> and M<sub>2</sub>. The masseteric scar normally extends to a point below the middle of M, but occasionally to a point below the anterior or the posterior roots

of that tooth. In most of the specimens the upper border of the masseteric scar is defined by a deep groove extending from the anterior end of the scar to the ascending ramus. In one specimen this groove is absent, and the scar is very faint. In all the specimens, except No. 8426, the jaws are approximately the same size, whereas this one specimen has an unusually large and deep jaw.

All of the upper teeth referred to Eumys nr. E. exiguus are closely similar to the type of Leidymys vetus Wood. In fact there is no question in my mind but that they represent the same species. Although no occlusal associations were found, there is little doubt that the upper and lower teeth assigned to Eumys nr. E. exiguus represent the same However, to refer all the material to L. vetus, when it so closely resembles the type specimen of Eumys exiguus, would imply that perhaps this species should be transferred to the genus Leidymys—a step that I am not prepared to take based solely on the evidence offered by the material from northeastern Colorado. Likewise, transferring L. vetus to the genus Eumys or making it synonymous with Eumys exiguus is unacceptable, because I think this small species is generically distinct from the species of Eumys but am not prepared to say whether or not it should be referred to Leidymys or to another genus.

# Eumys planidens Wilson

Figure 21

Eumys planidens Wilson, 1949, p. 48.

Type.—Univ. Colorado Mus. No. 19810; Cedar Creek member, White River formation, middle of W½ sec. 7, T. 11 N., R. 53 W., Logan County, Colorado.

Referred specimens.—From the type area and level; No. 8450; right jaw with I,  $M_1$ - $M_3$ . No. 8449; left jaw with  $M_1$ - $M_3$ .

TABLE 16.-Measurements (in mm.) of Eumys nr. E. exiguus and Eumys exiguus

							1	LOCAL	LITY	OF SI	PECIM	ENS					
11:			Col	orado							Neb	raska					South
		No 841			No. 8420					No. 8410			No. 8412				No. 12261
Crown length of M¹-M³. M¹, antero-posterior length M¹, transverse width M², antero-posterior length M², transverse width M³, antero-posterior length M³, transverse width		2.25 2.25 1.35 1.38 1.65 1.65 1.38 1.41 1.02 1.32							2,40 1.60 1.60 1.60	0 5 2 8			5.82 2.72 1.74 1.76 1.61 1.35 1.46				
	No. 8421	No. 8422	No. 8423	No. 8424	No. 8425	No. 8426	No. 537	No. 539	No. 540	No. 8411	No. 8413	No. 8414	No. 8415	No. 8416	No. 8417	No. 8418	
Crown length of M <sub>1</sub> -M <sub>8</sub> I, transverse width M <sub>1</sub> , antero-posterior length M <sub>2</sub> , transverse width M <sub>2</sub> , antero-posterior length M <sub>3</sub> , transverse width M <sub>8</sub> , antero-posterior length M <sub>8</sub> , transverse width	5.54 2.13 1.38 1.80 1.53 1.62 1.44	5.49 0.88 1.95 1.26 1.80 1.44 1.74 1.41	0.88 1.98 1.26 1.80 1.41	1.59 1.29 1.65 1.29	1.44		5.61 2.10 1.32 1.86 1.50 1.71	1.35 1.80	1.95 1.26 1.80	1.71 1.38 1.65 1.38	1.05 2.28 1.30 1.80 1.59	2.19	2.07 1.32 1.65 1.35	2.25 1.41 1.80 1.62	0.75 1.95 1.35	2.13 1.35 1.80 1.56	5.92 2.20 1.46 1.92 1.63 1.71 1.22

a. American Museum of Natural History. Type of Eumys exiguus.

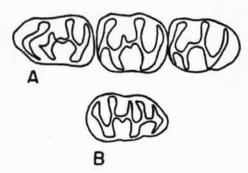


FIGURE 21.—Eumys planidens WILSON. (A) Occlusal pattern of M<sub>1</sub>-M<sub>3</sub> of No. 8449. (B) Occlusal pattern of M<sub>1</sub> of No. 8450. Approximately × 9.

To date the distribution of this species is limited to one exposure at a level about 90-100 feet below the top of the Cedar Creek member.

The additional specimens of this species add to our knowledge of the form. The first lower molar is now known, and the characters listed by Wilson as distinguishing the species are known to be more

than age characters.

As in other species of Eumys, M<sub>1</sub> is variable. In size and proportion (Table 17) it compares closely with other species of Eumys. The occlusal pattern is as follows: The anteroconid has buccal and lingual cingula. The anterior protoconid arm extends to the anteroconid, and the anterior metaconid arm crosses transversely to join the anterior protoconid arm. A variation of this part of the pattern is seen in specimen No. 8449 which has the anterior metaconid arm uniting with the anteroconid and has the anterior protoconid arm and the anterior lingual cingulum absent. The posterior protoconid arm is long and free, but closer to the metaconid than the entoconid. A mesoconid is present, but there is no mesolophid. The entoconid is expanded as in M<sub>2</sub> of the type specimen and is separated from the long posterolophid by a deep notch.

In individually older specimens, as in the younger type specimen, the lower incisor is slender and delicate, the crests of the molars are compressed, and the plane occlusal surface is retained. The most important point, perhaps, is the fact that the lingual cingulum on  $M_2$ - $M_3$  is absent consistently and never was present at any time, although a depression on the face of the tooth is often present at

TABLE 17.-Measurements (in mm.) of Eumys planidens

	No. 8450	No. 8449
Crown length of M <sub>1</sub> -M <sub>3</sub>	6.42	6.52
I, width at alveolus	0.85	9090909
M1, antero-posterior length		2.26
M1, transverse width	1.50	1.54
M2, antero-posterior length		2.00
Me transverse width	1.78	1.86
M <sub>3</sub> , antero-posterior length	1.95	2.20
M <sub>3</sub> , transverse width	1.75	1.76

this point. This is emphasized because Eumys brachyodus has an incipient lingual cingulum on M<sub>2</sub>-M<sub>3</sub>, which almost disappears with wear, but those teeth never completely lose all traces of the cingula. An interesting variation is present in M<sub>2</sub> of the two referred specimens. In them, the posterior protoconid arm does not extend transversely beyond the mesoconid crest, whereas the type specimen has this arm extending to the internal border.

# Eumys cf. E. planidens WILSON

Referred specimens. — Cedar Creek member (middle): No. 8472; left jaw with M<sub>1</sub>-M<sub>3</sub>; SW¼ sec. 2, T. 11 N., R. 54 W., Logan County.

W., Logan County.
Cedar Creek member (upper): No. 8467; left jaw with I,
M<sub>1</sub>-M<sub>2</sub>; NE¼ sec. 3, T. 11 N.. R. 54 W., Logan County.

No. 8472 possesses the major characters of *Eumys* planidens, but has larger, heavier teeth. It was obtained at approximately the same level as the type specimen.

No. 8467 has the narrow incisors, lack of anterior lingual cingulum, and other features of *Eumys planidens*, but the cusps and crests are heavier and thicker. It was found 20-40 feet below the base of the Whitneyan beds and high above the specimens from the middle part of the Cedar Creek member.

If these specimens represent a phylogenetic succession, the evolutionary change was rapid and parallels a related change in *E. elegans—E. brach-yodus* in many ways.

#### Eumys sp.

Referred specimen.—Cedar Creek member (lower): No. 8483; left jaw with M<sub>2</sub>-M<sub>3</sub>; W½ sec. 4, T. 11 N., R. 54 W., Logan County.

This specimen is an especially large, heavy jaw with large teeth (Table 18), but whether or not it is a large individual of a known species of Eumys or an unnamed kind remains to be seen. It has the fundamental Eumys pattern with the following characters: M<sub>2</sub> and M<sub>3</sub> with protoconids reduced, anterior lingual cingula weak, ectostylids weakly developed, spurs projecting posteriorly from anterior metaconid arms, weak anteriorly projecting spurs from posterior protoconid arms, mesoconids developed, no mesolophids, and posterolophids separated from entoconids by deep notches; metastylid between posterior protoconid arm and metaconid on M<sub>3</sub>; metaconid and entoconid of M<sub>2</sub>, and metaconid of M<sub>3</sub> high above plane of crests and other principal cusps; and masseteric scar reaching to anterior end of M<sub>2</sub>.

TABLE 18.—Measurements (in mm.) of Eumys sp.

	No. 8348
Crown length of M <sub>1</sub> -M <sub>3</sub> at alveolus	8.00
Incisor width back of alveolus	2.00
M2, antero-posterior length	2.60
M2, transverse width	2.40
M <sub>3</sub> , antero-posterior length	
M <sub>3</sub> , transverse width	2.45

#### Leidymys vetus Wood

Leidymys vetus Wood, A. E., 1937, p. 257.

Type.—AMNH No. 8742; middle Oligocene Cedar Creek beds of Colorado.

This species is discussed in the section on Eumus nr. E. exiguus.

# Variation among the Eumyine Rodents

Individual variation is an important item in any study of the species of Eumys. Literally, were one to conceive of every variation as having taxonomic value, there would be dozens of species. However, most of the Eumys material has been referred to E. elegans, unless there has been strong evidence for making additional species. To date only six species have been named, of which I think two, E. planidens and E. exiguus, may eventually be removed from the genus or at least separated subgenerically from each other and the other four. The remaining species, with the possible exception of E. parvidens, fall into one cline when considered in the light of stratigraphic and areal differentiation and constancy of qualitative and quantitative characters, as has been demonstrated in the discussion of the Eumys obliquidens-elegans-brachyodus complex. In each of these three species there were variants in characters other than those listed, and undoubtedly some workers would argue for different species because of these variations. To use one variation to define a species would suggest treating other variations in the same manner and, in the end, would result in breaking down the criteria established for the already existing species.

There were too few upper teeth for a proper study, but as a result of the examination of the series of lower jaws from northeastern Colorado, I would evaluate the characters of the teeth thus: No particular character is of great value unless it has a restricted stratigraphic range or lacks quantitative overlap. In conjunction with the above, the following seems evident: Presence or absence of cingula, good. Strength of development of cingula, poor except in Eumys brachyodus. Protoconid arm direction, good. Presence of anterior protoconid and metaconid arms may be good if consistent and correlated with other reliable characters, but present evidence shows much variation. Extra cuspules, crests, spurs, or variation in position of union of cusps, spurs, and lophids, especially on M<sub>3</sub>, appear valueless at present. This is also true concerning the upper teeth, especially M3. The mesolophids are the last of the variable structures to be lost or reduced; that is, they lag behind other changing characters, as may be noticed in E. elegans which retained well-developed mesolophids as a variant after the other E. obliquidens characters ceased to appear, and were retained as a variant in later E. elegans specimens after the E. brachyodus characters had appeared.

I think that any future modification of the taxonomy must be by the standards proposed and not by the method of collecting together a group of similar specimens and naming it as new without regard for intergradation or variation.

#### Order CARNIVORA Bowdich, 1821

## FAMILY HYAENODONTIDAE LEIDY, 1869

Hyaenodon horridus and H. crucians were listed by Cope (1874, p. 9) as present in northeastern Colorado. H. cruentus was reported by MATTHEW (1909, p. 105), and in this paper H. mustelinus is added to the faunal list. The specimens of H. crucians and H. mustelinus in the University of Kansas Museum of Natural History are typical, but there is difficulty in interpreting size range, secondary sexual differences, and structural variations in specimens of Hyaenodon cf. H. cruentus and H. horridus. Specimens larger than H. crucians, but having short faces, are assigned to H. cf. H. cruentus. Specimens larger than H. cf. H. cruentus, and having a normal length of face, are assigned to H. horridus. Nevertheless, in both groups the specimens are consistently smaller when compared with specimens of the two species from other areas.

## Hyaenodon horridus Leidy

Hyaenodon horridus Lemy, 1853, p. 392,

Referred specimens. — Cedar Creek member (middle): No. 8138; crushed anterior part of skull; sec. 3, T. 11 N., R. 54 W., Logan County. Cedar Creek member (upper): Univ. Colorado Mus. No. 19865; crushed skull; SE½ sec. 8, T. 11 N., R. 53 W., Logan

County.

These two skulls are referred to this species primarily on the basis of large size. Both specimens seem to be smaller, however, than the average for Hyaenodon horridus.

The skull in the University of Colorado Museum came from a level a few feet below the contact of the Orellan and Whitneyan beds.

# Hyaenodon cf. H. cruentus Leidy

Referred specimens. — Cedar Creek member (middle or upper): Nos. 141, 4975; incomplete skulls; possibly from or near sec. 16, T. 11 N., R. 53 W., Logan County.

The skulls of these two specimens, in the parts that can be measured, are larger than any skulls of Hyaenodon crucians examined by me but are smaller than the two skulls from northeastern Colorado which were referred to H. horridus. When compared with skulls from other areas, it may be seen that Nos. 141 and 4975 are intermediate in size between large skulls of *H. crucians* and those of H. cruentus. Besides over-all size, No. 141 and No. 4975 differ from typical H. cruentus as follows: the premolars are the size of those in H. horridus; the molars are the size of those in H. crucians; and the muzzle is shorter than that of H. horridus.

#### Hyaenodon crucians Leidy

Hyaenodon crucians LEIDY, 1853, p. 393.

Referred specimens.—Cedar Creek member (lower): Univ. Colorado Mus. No. 19862; fragment of right jaw with M<sub>1</sub>-M<sub>2</sub>; SW¼ sec. 12, T. 11 N., R. 54 W., Logan County. No. 8139; skull and jaws; SW¼ sec. 21, T. 11 N., R. 53 W., Logan County. No. 8140; fragment of right jaw with M<sub>2</sub>-M<sub>3</sub>; same locality as No. 8139.

The size and other characters of Nos. 8139 and 8140 agree with the type specimen and with the description of the species given by Scott & Jepsen (1936, p. 50). The specimen in the University of Colorado Museum is immature but seems to be referable to this species.

# Hyaenodon mustelinus Scott

Huaenodon mustelinus Scott, 1894a, p. 499.

Referred specimen.—Cedar Creek member (lower): No. 8142; incomplete skull and jaws; SE¼ sec. 31, T. 12 N., R. 54 W., Logan County.

Although the one specimen known from northeastern Colorado is slightly smaller than the specimens described by Scott (1894a, p. 499) and Scott & Jepsen (1936, p. 53), there is little reason to question its reference to Hyaenodon mustelinus.

#### FAMILY CANIDAE GRAY, 1821

# Pseudocynodictis paterculus (MATTHEW)

Cynodictis paterculus MATTHEW, 1903, p. 209. Pseudocynodictis paterculus, CLARK, 1937, p. 312.

THORPE (1922, p. 428) referred specimens in the Marsh Collection from northeastern Colorado to this species.

#### Pseudocynodictis nr. P. paterculus (MATTHEW)

Referred specimens.—Horsetail Creek member: No. 8173; three fragments of jaws. No. 8174; right jaw fragment with P<sub>4</sub>-M<sub>1</sub>. No. 8175; left jaw fragment with P<sub>4</sub>-M<sub>3</sub>. No. 8176; left jaw fragment with M<sub>1</sub>-M<sub>2</sub>. Above specimens from NE¼ sec. 31, T. 11 N., R. 56 W., Weld County. No. 8179; left P<sub>4</sub>-M<sub>2</sub>; N½ sec. 33, T. 11 N., R. 53 W., Logan County.

These specimens have several characteristics in which they differ from Pseudocynodictis gregarius and seem close to P. paterculus. Compared to P. gregarius: the talonid of M1 is higher, and the cusps are more pronounced; M<sub>2</sub> is longer, the basin of the talonid is broader, the hypoconid is higher and more bladelike, and the protoconid and metaconid are much higher than the paraconid; M<sub>3</sub> is larger, and the cusps are more pronounced. On the other hand, the shearing blade of M, does not seem to be more transversely directed than in P. gregarius, although the blade is directed more transversely in P. paterculus. These specimens seem to represent a stage intermediate between P. paterculus and P. gregarius.

# Pseudocynodictis gregarius (COPE)

Canis gregarius COPE, 1873b, p. 3. Pseudocynodictis gregarius, Schlosser, 1902, p. 50.

Type.—AMNH No. 5297; Tertiary of Colorado.

Referred specimens.—Cedar Creek member (lower): No. 8177; left M2; SW% sec. 12, T. 11 N., R. 54 W., Logan County.

Cedar Creek member (middle): No. 8183; rear part of skull with M¹; W½ sec. 7, T. 11 N., R. 53 W., Logan County. No. 8186; left P<sub>4</sub>-M<sub>1</sub>; E½ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8187; left ramus with C, P<sub>1</sub>, P<sub>4</sub>-M<sub>3</sub>; SE¼ sec. 31, T. 12 N., R. 54 W., Logan County. No. 8194; right P<sub>4</sub>-M<sub>2</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County.

It is realized that the species of the genus Pseudocynodictis have not been adequately characterized. Secondary sexual differences, size range, and stratigraphic position are three items that need to be clarified for the species already named before any more closely related species are described. Stratigraphy is no problem and will go far toward solving the problem of size range if, in the future, collections are made with care to eliminate false associations.

A series of Pseudocynodictis specimens ranging from small to large in size are present in the northeastern Colorado Orellan beds. These tend to fall into size groups which are not satisfactorily distinguished in all cases by other features such as structure, locality, or stratigraphic level. Perhaps more exact collecting or better specimens would aid in distinguishing these groups. In this paper, these groups are referred to: P. lippincottianus (large), P. gregarius (medium, but tending to divide into two groups), and Pseudocynodictis sp. (small). The specimens assigned to P. gregarius can be divided into deep-jawed forms and shallow-jawed forms, which may represent males and females of that species. Because of structural differences, it is unlikely that one group represents females of P. lippincottianus and the other group represents males of the small unnamed species.

#### Pseudocynodictis lippincottianus (COPE)

Canis lippincottianus Cope, 1873c, p. 9. Pseudocynodictis lippincottianus, Schlosser, 1902, p. 50.

Type.—AMNH No. 5327; Tertiary of Colorado.

Referred specimens.—Cedar Creek member: No. 120; left lower jaw with C, P<sub>3</sub>-M<sub>2</sub>; sec. 16, T. 11 N., R. 53 W., Logan County. No. 137; skull and jaws; near sec. 28, T. 11 N., R. 53 W., Logan County. No. 8191; maxillary fragment with left M¹-M²; SW¼ sec. 21, T. 11 N., R. 53 W., Logan County. No. 8196; left jaw with C, P<sub>2</sub>, P<sub>4</sub>-M<sub>1</sub>; E¾ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8199; right jaw with P<sub>1</sub>-M<sub>2</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County. Cedar Creek member (upper): No. 8200; fragment of

Cedar Creek member (upper): No. 8200; fragment of left jaw with M<sub>1</sub>; NE¼ sec. 3, T. 11 N., R. 54 W., Logan

I agree with Hough (1948, p. 590) that this species is distinct from Pseudocynodictus gregarius but, because of the indeterminate nature of Marsh's

specimen, doubt the advisability of making P. lippincottianus a synonym of P. angustidens (MARSH). COPE (1873c, p. 9) based P. lippincottianus on material collected in northeastern Colorado, but he was somewhat doubtful of its validity. The specimens listed above agree with the description of the type given by COPE and differ in several particulars from specimens of Pseudocynodictis gregarius from the same area. The skull referred to P. lippincottianus is damaged and slightly compressed, but certainly its over-all length was at least 100 mm. and possibly as much as 110 mm. The upper teeth are damaged or missing with the exception of P1 and P2, which are similar to those of P. gregarius. No. 8191, a left maxillary with M1-M2, has been tentatively referred to P. lippincottianus. If this reference is correct, then M1 and M2 of P. lippincottianus are relatively wider than the corresponding teeth of P. gregarius (Table 19). The lower jaw of P. lippincottianus has the vascular impression or notch very deep and distinct, starting at an acute angle directly below the third molar. The lower molars of P. lippincottianus are relatively longer in relation to the premolars than in P. gregarius. The hypoconid of M, is low, more like that of Daphoenus than that of P. gregarius.

That Pseudocynodictus lippincottianus may represent the males of the species P. gregarius seems unlikely since the latter species is about five times as common as the former. Also, there are localities where P. gregarius is common but P. lippincottianus is absent. In the light of our knowledge of present day canids, it seems improbable that certain areas

would be inhabited only by females.

Table 19.—Measurements (in mm.) of Pseudocynodictis lippincottianus

	No. 120	No. 8197	No. 8191	No. 137
Length of skull	****			100-110
M <sup>1</sup> , antero-posterior length	1879.004	*:0:00	7.0	7.6
M1, transverse width		10 - 10	11.0	
M <sup>2</sup> , antero-posterior				
length	4 5 4 4	****	4.2	40000
M <sup>2</sup> , transverse width	4 2 4 4		6.8	
Posterior border of lower				
canine to rear of M3	44.7	44.2	5.000	42.0
Length of lower molars	19.8	20.2	(31.543.53)	19.3
Length of lower premolars	24.0	23.4	7.6.409.40	21.7

# Pseudocynodictis temnodon (WORTMAN & MATTHEW)

Cynodictis temnodon Wortman & Matthew, 1899, p. 180. Pseudocynodictis temnodon, Matthew, 1918, p. 189.

MATTHEW (1901, p. 357) referred a specimen from the Leptauchenia zone in Logan County to this species.

# Pseudocynodictis sp. (Small form)

Referred specimens. — Cedar Creek member (middle): No. 136; left lower jaw with P<sub>2</sub>-M<sub>2</sub>; Logan County. No. 8201; skull and jaws; sec. 22, T. 11 N., R. 52 W., Logan County. No. 8202; left M<sub>1</sub>; SE½ sec. 31, T. 12 N., R. 54 W., Logan County. No. 8203; right M<sub>1</sub>-M<sub>2</sub>; E½ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8204; anterior end right ramus with C, P<sub>3</sub>; E½ sec. 3, T. 11 N., R. 54 W., Logan County. No. 8208; left lower jaw with M<sub>2</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County.

These small jaws and one crushed skull and jaws may represent an unnamed species of the genus *Pseudocynodictis*.

#### Parictis nr. P. dakotensis CLARK

Referred specimen.—Horsetail Creek member: No. 8168; fragment of jaw with heel of  $M_1$  and  $M_2$ ; N½ sec. 33, T. 11 N., R. 53 W., Logan County.

In size and appearance this specimen corresponds closely to the description of *Parictis dakotensis* CLARK. Both teeth have a rugose surface. The heel of M, is basined, the entoconid is higher than the hypoconid, and a well-developed fossa is present at the rear of the tooth. M2 is practically unworn, hence revealing the pattern of the tooth, the structure of which has been poorly known. The trigonid is small and not so high as the heel of M<sub>1</sub>. The metaconid is the highest and largest of the cusps; the protoconid is slightly anterior to the metaconid; and the paraconid is reduced to a vestigial cusp. Crests connect all three cusps which are set close together. On the antero-external surface of the trigonid, the cingulum swells into a plump, low cusp. This enlargement of the external side of the tooth has caused the protoconid to appear almost median in position.

#### Daphoenus cf. D. vetus Leidy

Referred specimen.—Cedar Creek member (middle): No. 8207; anterior part of right jaw with P4; NW¼ sec. 3, T. 11 N., R. 54 W., Logan County.

#### Daphoenus hartshornianus (COPE)

Canis hartshornianus Cope, 1873c, p. 9. Daphoenus hartshornianus, Scorr, 1898, p. 361.

Type.—AMNH No. 5296; Tertiary of Colorado.

Referred specimens. — Cedar Creek member: No. 122; part of right lower jaw with M<sub>1</sub>-M<sub>2</sub>; Chimney Canyon, sec. 3, T. 11 N., R. 54 W., Logan County. No. 165; part of left lower jaw with M<sub>2</sub>-M<sub>3</sub>; same locality as No. 122. No. 8205; part of right lower jaw with P<sub>4</sub>-M<sub>2</sub>; W½ sec. 7, T. 11 N., R. 53 W., Logan County. No. 8106; right M<sub>1</sub>; locality same as No. 8205.

The stratigraphic assignment of specimens No. 122 and No. 165 is based on H. T. MARTIN's field notes for the year 1925.

#### Proamphicyon cf. P. nebraskensis HATCHER

Referred specimen. — Cedar Creek member: No. 138; right lower jaw with P<sub>1</sub>, M<sub>1</sub>-M<sub>2</sub>; "north of Stone Ranch"

(fide H. T. MARTIN, 1925 field notes). This locality probably is in T. 12 N., R. 55 W., Logan County.

This specimen compares closely with Walker Museum specimen No. 1426, considered by Hough (1948, p. 592) to be conspecific with the type. Good occlusion is made with the teeth in a cast of the type skull.

## Daphoenocyon? cf. D. dodgei (Scott)

Referred specimen. - ?Cedar Creek member: No. 102; part of left lower jaw with P2-P4; northeastern Colorado.

This specimen has blunt, broad premolars and a deep ramus like specimen No. 1456 in the Walker Museum. Hough (1948, p. 595) referred No. 1456 to D. dodgei.

# FAMILY MUSTELIDAE SWAINSON, 1835 Palaeogale lagophaga (COPE)

Bunaelurus lagophagus Cope, 1873c, p. 8. Palaeogale lagophaga, Simpson, 1946, p. 12.

Type.—AMNH No. 6812.

Referred specimens. — Cedar Creek member: No. 41; right jaw fragment with M<sub>1</sub>; Logan County. No. 8166; left jaw with M<sub>1</sub>; W<sub>2</sub> sec. 7, T. 11 N., R. 53 W., Logan County.

MATTHEW (1902, p. 140) states that Cope's type came from beds 50 miles east of Pawnee Buttes, which would place the locality in eastern Logan County. This may have been a slight overestimation of the distance, but it does indicate that the locality was some distance east of Pawnee Buttes. SIMPSON (1946, p. 4) lists four specimens (including Cope's type) from northeastern Colorado and refers all to Palaeogale lagophaga and to an Orellan age.

# FAMILY MUSTELIDAE SWAINSON?, 1835

In 1925 Mr. H. T. MARTIN obtained a lower jaw of a carnivore in "Chimney Canyon," Logan County, Colorado, which he listed in his field notes as "83-B [B refers to beds of Orellan age, E. C. G.]—Cynodictis underjaw. lower levels. HM." This specimen, so labeled, remained unnoticed in the University of Kansas collections until recently and is now the type of the following new genus and species.

#### DRASSONAX, new genus

Type species.—Drassonax harpagops.

Distribution.—Cedar Creek member of the White River formation, northeastern Colorado.

Diagnosis.—Mandible short, heavy, and massive; incisors crowded; premolars cingulated, broad, and without accessory cusps; metaconid of M, reduced; trigonid of M2 small; dental formula 3, 1, 4, 3.

# Drassonax harpagops, new species

Figure 22

Holotype. - Left lower jaw with C-M2, No. 121, Vert. Paleont. Coll., Univ. Kansas Mus. Nat. Hist.

Geological age and locality.—Silts of Orellan age in the Cedar Creek member of the White River formation in "Chimney Canyon," sec. 3, T. 11 N., R. 54 W., Logan County, Colorado.

Diagnosis.—As for the genus.

Description.—The type is a left ramus lacking only the incisors, M<sub>s</sub>, tip of the coronoid process, and external end of the mandibular condyle. Its size (Table 20) is about that of the lower jaw of Recent Martes caurina origenes (RHOADS). Foramina are present on the external surface of the body of the ramus below P1, below the space between P1 and P2, and below the anterior root of P3. The masseteric fossa is deep and reaches forward to M2. The anterior border of the ascending ramus is steep, more like that of the procyonids than of the mustelids, and the antero-internal border is buttressed by a ridge rising from the anterior end of the scar for the temporal muscle. The mandibular condyle of this specimen is especially remarkable in its massiveness and vertical depth. This vertical depth is 4.7 mm., almost twice the depth of the mandibular condyles in comparable-sized Martes, and equal to the condyle of male Martes p. pennanti (ERXLEBEN), an animal with a jaw almost twice the size of the type of Drassonax harpagops. Unfortunately, the complete condyle is not preserved. However, by comparison of width and depth, and angle of the transverse axis of the condyle in relation to the jaw with similar characters in other mustelids, it appears reasonable to assume that the maximum condylar width did not exceed 16 mm. Furthermore, the postero-inferior part of the articulating surface of the condyle gives evidence that the width was be-tween 13 and 14 mm. This is in keeping with the proportions found in *Plesiogulo*. The relationship of the transverse axis of the condyle to the rest of the jaw gives evidence that the animal was broad skulled like *Plesiogulo*. The scars where ligaments attached around the neck and internal end of the condyle are large and prominent. Compared with many mustelids, the condyle is high on the ascending ramus, being at the level of the tooth row. The angular process is deep and marked by well-developed muscle scars. The symphyseal scar involves the whole anterior end of the internal surface of the jaw and extends posteriorly to the posterior end of P2.

The dental formula is 3, 1, 4, 3. The tooth row is curving, with a change of direction in the longitudinal axis of P1-P3 and M1-M2 in relation to P4. Although this change of direction is difficult to detect without careful inspection, it does foreshadow the type of curve found in Plesiogulo and is associated with broad skulls. The change of direction is not like that seen in Recent Martes, which is caused by crowding of the teeth and shortening of

the jaw.

The presence of all three incisors is uncertain. Although the end of the mandible is preserved in

good condition and the alveoli of two incisors are plainly visible, it is possible that a minute pit below the alveolus of the median incisor is not the alveolus of a vestigial first incisor. The alveolus of the second incisor shows that the root was compressed laterally, whereas the alveolus of the third incisor is round. This lateral alveolus, containing the root of the incisor, is below the level of the second incisor and lies next to the infero-internal side of the canine. The crowded condition of these incisors resembles that seen in some extreme cases of crowding found in Recent martens.

The canine is large in diameter, and, although the tip is missing, it appears to be short. It lacks the swelling below the alveolar border that is char-

acteristic of many mustelids.

Only the third and fourth premolars are set close together. All have thick cusps, cingula completely surrounding the bases of the teeth, and no accessory cuspules. With the exception of P<sub>1</sub>, all the premolars are double rooted. The enamel surfaces of the premolars are faintly rugose and, to a lesser degree, so are the molars, but not to the extent seen in specimens of *Parictis* Scott. Well-developed carinae are present, anteriorly and posteriorly, on all the premolars except P<sub>1</sub>, which lacks the anterior one. P<sub>1</sub> is reduced. P<sub>2</sub> is noticeably larger than P<sub>1</sub> and possesses a relatively longer heel than do any of the other premolars. P<sub>3</sub> is slightly larger than P<sub>2</sub>, the apex of the principal cusp is more centrally located, and the heel turns outward where it ex-

Table 20.—Measurements (in mm.) of Drassonax harpagops

No. 121
Ė
lean an
54.7
8.4
8.7
9.9
5.0
4.7
10.9
10.0
15.0
36.2
18.4
11.9
29.5
3.99
3.69
2.50
1.80
3.59
2.27
4.79
2.50
5.90
3.01
8.00
4.05
3.58
3.90
2.89

tends slightly beyond the anterior end of P<sub>4</sub>. P<sub>4</sub> is like P<sub>3</sub> except that it is much larger and lacks the postero-external bulge of the heel, but it does extend posteriorly beyond the anterior end of M...

tend posteriorly beyond the anterior end of  $M_1$ . The trigonid of  $M_1$  is slightly higher than  $P_4$ . The paraconid is short, stubby, and separated from the protoconid by a small, narrow notch. The protoconid is thick and heavy with the apex of the cusp lateral in position and in line antero-posteriorly with the hypoconid. The protoconid is separated from the metaconid by a minute notch. The metaconid is reduced, but relatively not so much as in Plesiogulo marshalli (MARTIN), yet more so than in Mionictis incertus (MATTHEW). The cingulum is not so conspicuous on M<sub>1</sub> as it is on the premolars. Its best development is seen on the antero-external surface of the tooth where it reaches from the lateral side of the protoconid to the anterior end of the tooth; between the metaconid and paraconid; and on the external side of the heel. The heel of M<sub>1</sub> is short and has the hypoconid and entoconid cusps elongated to form ridges of about equal height, which have converted the heel into a basin that is open posteriorly. Each ridge is separated from the protoconid or metaconid by a slight notch. A facet of wear on the postero-external surface of the heel might be interpreted as indicating that the M1 yet retained a well-developed metacone.

M<sub>2</sub> is reduced, its crown is oval, and its pattern is intermediate between that of the primitive canid and that of a typical mustelid. The protoconid and metaconid cusps are marginal, and the smaller metaconid is anterior to the protoconid. A crest connects the two cusps. The paraconid is absent. The hypoconid is large and prominent. The large, basined heel is formed by a crest between the hypoconid and protoconid, together with the rim of the heel extending from the hypoconid to the metaconid. The crests between the protoconid and metaconid, and protoconid and hypoconid still retain minute traces of the notches that formerly sepa-

rated these cusps.

The alveolus alone represents  $M_3$  in this specimen, but it shows that the tooth was reduced and crowded between  $M_2$  and the ascending ramus. It had not, however, reached the stage represented by the infrequently occurring  $M_3$  in Recent *Martes* and probably was a constant part of the dentition.

Discussion.—This jaw resembles mustelid lower jaws, both fossil and Recent, more than it does the lower jaws of other carnivores in the following combination of characters: (1) crowded incisors, (2) blunt, wide, completely cingulated premolars that lack accessory cuspules, (3) reduced metaconid and talonid of  $M_1$ , (4) reduced talonid and height of trigonid of  $M_2$ , (5) probable reduced size of  $M_3$ , and (6) short, massive mandible with deep, large masseteric fossa. The incisors of this specimen appear much like mustelid incisors in the pattern of their crowding, the reduction of the root of

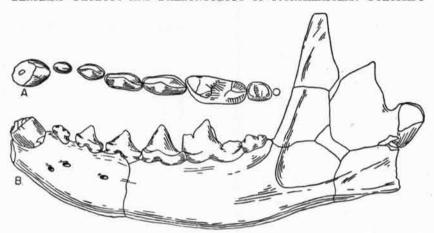


Figure 22.—Drassonax harpagops, n. gen. and sp. No. 121. (A) Occlusal view of left C-M<sub>2</sub>. (B) External view of left jaw with teeth. Approximately  $\times$  2.

the first tooth, the lateral compression of the root of the second, and the retention of a rounded root in the third. The simplicity of the lower premolars, which Matthew (1924, p. 129) considered to be a characteristic of the mustelids, is, in Drassonax, in direct contrast to the usual canid condition where accessory cuspules are common. The M1 with its short, narrow heel and reduced metaconid shows a musteline pattern. The tendency for reduction of the lower molars, another mustelid characteristic, would suggest that this specimen is a mustelid and would also eliminate this specimen from an ancestral position for several of the later groups of mustelids. After the lower premolars, the second lower molar probably is next in importance in taxonomic significance. The trend in post-carnassial musteline molars, of course, is reduction, and in the second lower molar there also appear at least two additional trends: (1) the tendency to develop a longitudinal shearing blade, and (2) the tendency of the tooth to round out its shape by expansion of the trigonid and reduction of the talonid. This latter feature, when coupled with the formation of a transverse crest from protoconid to metaconid cusps that are marginal in position, tends to obscure the longitudinal shearing blade. M2 of Drassonax shows the beginning of this second trend, which is not seen in the canids. The third lower molar is not present, but apparently it is small. To state that this specimen is not a mustelid because of the presence of an M<sub>3</sub> would be unwarranted. limit mustelids to groups that lacked M<sub>s</sub> implies that the loss of M, was the first mustelid character to appear - a restriction opposed by the occasional presence of a minute M<sub>3</sub> in Recent mustelids. combination of characters serves to diagnose the mustelids, and these characters presumably did not appear simultaneously. The mandible, particularly the masseteric fossa and ascending ramus, is much more like those of mustelids than those of canids, especially Oligocene canids, in its form.

Granting that *Drassonax* is a mustelid, the phyletic position of the genus in the family is not questionable. The trend of the M<sub>1</sub> toward reduction of the metaconid cusp, reduction of the heel, and lateral narrowing of the tooth would require reversal for the genus to fit into the phyletic line of any mustelid subfamily except the Mustelinae. Comparison of this specimen with other fossil mustelids eliminates from consideration as possible relatives all forms except the wolverine-like forms of the subfamily Mustelinae—the relationship being closer to *Plesiogulo* than to any of the others.

The presence of Drassonax in the middle Oligocene, together with Palaeogale, indicates that there were at least two branches of mustelid development at that time. Obviously Palaeogale was far ahead of Drassonax in jaw reduction and tooth modifica-That there were other separate branches or phyletic lines is even more evident in the post-Oligocene fossils. There have been classifications that reflected these phyletic branches (SIMPSON, 1945, p. 113), but SIMPSON rejected the arrangements and used the grouping Mustelinae Gill because he thought that the evidence did not warrant a division at present. In my opinion, the new genus, Drassonax, lends weight to the case for establishing at least a gulonine branch but, at the same time, suggests that the genera of the Mustelinae are more closely related to each other than to other groups. SIMPSON has commented (1945, p. 227) upon a possible cause for the difficulties in the mustelid classification—an explosive and rapid divergence of the mustelid stem stock into many phyletic lines, a pattern similar to that followed by the rodents.

Unfortunately, at present this new genus only adds to the heterogeneous nature of the Mustelinae. The conclusion that it shows the existence of another line of mustelids in addition to the weasel-like forms in the Orellan Oligocene, and that it may be ancestral to the wolverine group must be considered as a tentative conclusion which cannot be

verified until the skull is known.

# FAMILY FELIDAE GRAY, 1821 Dinictis squalidens (COPE)

Daptophilus squalidens Cope, 1873b, p. 2. Dinictis squalidens, Cope, 1879, p. 170.

Type.—AMNH No. 5335; Cedar Creek area, northeastern

MATTHEW (1901, p. 390) referred to this species specimens from the "Cedar Creek beds" of Colorado.

#### Dinictis felina LEIDY

Dinictis felina LEIDY, 1854a, p. 127.

Referred specimen.—?Cedar Creek member: No. 5045; fragment of jaw with P4; near sec. 9, T. 11 N., R. 55 W., Logan County.

MATTHEW (1901, p. 389) at first inferred that a species of *Dinictis* larger than *D. squalidens* was to be found in northeastern Colorado, and he later (1910a, p. 310) reported *D. felina* to be present in the Orellan beds.

Although No. 5045 is referred to this species, it is possible that it is a large individual of *D. squalidens*.

#### Dinictis sp.

Referred specimens.—Horsetail Creek member: No. 9787; fragment of right jaw with M<sub>1</sub>; W½ sec. 16, T. 10 N., R. 51 W. Logan County.

W., Logan County.
Cedar Creek member (middle): No. 8137; incomplete left jaw with damaged teeth; SW4 sec. 25, T. 12 N., R. 54 W., Logan County.

The tooth from the Horsetail Creek member is near *Dinictis squalidens* in size but has a betterdeveloped metaconid and heel than is seen on Orellan specimens of this species.

No. 8137 is unusual in that, although in size it agrees with small individuals of *Dinictus squalidens*, it has only an incipient flange developed for protection of the upper canine. It and the specimen referred to *D. felina* demonstrate the need for a study and review of this genus in respect to stratigraphic distribution and to individual and geographic variation.

## Hoplophoneus primaevus (Leidy & Owen)

Machairodus primaevus Leidy & Owen, in Leidy, 1851c, p. 329.

Hoplophoneus primaevus, Cope, 1880, p. 841.

Referred specimen.—?Cedar Creek member: No. 179; damaged skull; Logan County, Colorado.

The specimen listed above is considered to be Hoplophoneus primaevus, based on Simpson's (1941) review of the genus. This genus is rare in northeastern Colorado. Cope (1874a, p. 509) mentioned two specimens—the type of H. oreodontis and a referred individual. Matthew (1901, p. 394) listed a skull as agreeing in form and measurements with Leidy's type of H. primaevus, and a jaw as corresponding closely to specimens of H. robustus. Simpson considers all this material to be H. primaevus, and Hough (1949) supports this view.

# ORDER PERISSODACTYLA OWEN, 1848 FAMILY EQUIDAE GRAY, 1821

# Mesohippus proteulophus Osborn

Mesohippus proteulophus Osborn, 1904, p. 171.

Referred specimens.—Horsetail Creek member: No. 9789; right upper molar; W½ sec. 16, T. 10 N., R. 51 W., Logan County. No. 9790; right upper molar; S½ sec. 36, T. 10 N., R. 59 W., Weld County. No. 9124; fragment of jaw with P4; N½ sec. 31, T. 11 N., R. 56 W., Weld County.

The hypostyles of Nos. 9789 and 9790 are smaller and simpler than the hypostyles in most specimens of Mesohippus eulophus, being intermediate in development between the condition in M. eulophus of the Orellan and that described by Osborn for M. proteulophus of the Chadronian. Reference of the specimens to M. proteulophus is based on the probability that M. proteulophus has as wide a range of variation of the hypostyle as does M. eulophus. Furthermore, I feel that the Chadronian members of this chronocline should bear the same name.

## Mesohippus eulophus Osborn

Mesohippus eulophus Osborn, 1904, p. 173.

Type.—AMNH No. 8791; upper Oreodon zone (Horizon B) of Cedar Creek, Colorado (fide Osborn, 1918).

Referred specimens. — Cedar Creek member: No. 9045; right P³-P⁴, M²; sec. 22, T. 11 N., R. 52 W., Logan County. No. 9046; left P⁴-M²; SW¼ sec. 21, T. 11 N., R. 53 W., Logan County. No. 9047; right lower jaw with P₂-M₂; W¾ sec. 7, T. 11 N., R. 53 W., Logan County.

Cope (1874, p. 9) considered Mesohippus bairdii Leidy to be present in northeastern Colorado, and, in addition, he later (1874a, pp. 496-497) recognized two other species, M. exoletus (Cope) and M. cuneatus (Cope). Matthew (1901, p. 357) at first recognized only M. bairdii, but later (1909, p. 106) questioned the presence of M. bairdii and listed M. eulophus Osborn and M. exoletus. Osborn (1918, p. 50) still later stated that Matthew considered M. eulophus to be a subspecies or geographic variation of M. bairdii. At that time, Osborn considered Cope's species to be indeterminate because the types were lost.

The determinable specimens found in the Cedar Creek by me are similar to the type of Mesohippus eulophus, and they have been referred to this species. However, the specimens match equally well the description of M. exoletus by COPE. With this material at hand, it is rather difficult to understand OSBORN'S treatment of Cope's species, since the description of M. exoletus by Cope contained enough information to make it the basis for a species distinguishable from M. bairdii. A solution to the problem of the synonymy of M. exoletus and M. eulophus probably can be reached by studying large populations of M. bairdii and determining its range of variation. Following such a study, were the description of M. exoletus still sufficient to distinguish the northeastern Colorado forms, then

there would follow the problem of deciding whether or not *M. exoletus* and *M. eulophus* are synonymous. For these reasons I have considered it best to continue to use Osborn's name, especially since there is

a type specimen available for comparison.

In addition to those listed above, there are many specimens consisting of isolated teeth and several without adequate stratigraphic records. From the combined material the following generalizations concerning Mesohippus eulophus may be made: (1) all the teeth are larger than those of M. bairdii; (2) an internal cingulum is present on the upper (2) an internal cingulum is present on the upper teeth; (3)  $P^4$  is wider than  $M^1$ ; (4)  $P^1$  is reduced more than in M. bairdii; (5) the metaconule is not prominent (isolated on  $P^2$  of one specimen); (6) the protoconule is well defined and prominent; (7) the parastyle and mesostyle are very strong; (8) the metastyle is weak or absent; (9) the hypostyle is strong; (10) the metaloph tends to fuse with the hypostyle with wear; (11) the parastyle and paracone are united to the protoloph; (12) there is no definite crochet, but occasionally incipient ones; (13) the maximum transverse diameter of the lower teeth is at P<sub>3</sub>-P<sub>4</sub>. Some of these characters differ from those listed by Osborn in diagnosing M. eulophus. Osborn stated that the molars were wider than the premolars and that the protoconule was faint. There is not much question about the large size of the last two lower premolars. They resemble specimens of Miohippus in that respect. P4 is as wide as M1, and wider in some specimens. The range in diameter is so narrow, however, that variations undoubtedly exist in which the P4 may have a smaller transverse width. Whether the protoconule should be described as faint or strong appears to depend upon what specimens are used. The fact that the protoloph and metaloph are continuous might tend to make the protoconule less conspicuous than in Mesohippus bairdii, for example, but it certainly does not obliterate the conule in any way. Most of the characters show that these specimens are different from M. bairdii and indicate an advance over that species toward Miohippus.

#### Mesohippus sp.

Referred specimens.—Horsetail Creek member: No. 9119; fragments of lower teeth; W½ sec. 9, T. 10 N., R. 51 W., Logan County.

These equid remains suggest that a species smaller than *Mesohippus proteulophus* is also present in the Horsetail Creek member.

#### Miohippus sp.

Referred specimen.—?Vista member: No. 4901; part of right jaw with P<sub>3</sub>-M<sub>1</sub>, M<sub>3</sub>; sec. 3, T. 11 N., R. 54 W., Logan County.

This specimen was collected by H. T. MARTIN in 1925 at Chimney Canyon in Logan County. In color and preservation this specimen resembles the material from the Vista member at this locality. The teeth are comparable in size with those of *Miohippus meteulophus* and are much larger than any specimens of *Mesohippus* from the Cedar Creek member.

Small fragments of teeth have been found by me in the Whitneyan beds, but nothing that is generi-

cally determinable.

## FAMILY BRONTOTHERIIDAE MARSH, 1873

# Megacerops acer (COPE)

Megaceratops acer Cope, 1873a, p. 4. Megacerops acer, Osborn, 1929, p. 545.

Type.—AMNH No. 6348; Chadron formation, Horsetail Creek, northeastern Colorado (fide Osborn, 1929).

This species is cited because of the good skeletons from Weld County in the Denver Museum of Natural History.

Scott (1941, p. 910) was of the opinion that the genus Brontops Marsh was also represented in

northeastern Colorado.

Fragments of teeth referable to the Brontotheriidae have been found in the W½ sec. 9, T. 10 N., R. 51 W.; and NE¼ sec. 31, T. 11 N., R. 53 W., Logan County, and in the N½ sec. 31, T. 11 N., R. 56 W., Weld County. A lower jaw from the S½ sec. 1, T. 11 N., R. 54 W., Logan County, appears to be close to Megacerops.

#### FAMILY HYRACODONTIDAE COPE, 1879

#### Hyracodon nebraskensis LEIDY

Rhinoceros nebraskensis Leidy, 1850a, p. 121. Hyracodon nebraskensis, Leidy, 1856a, p. 92.

Referred specimen.—Cedar Creek member (middle): No. 9050; maxillaries, jaws, and limb bones; E½ sec. 12, T. 11 N., R. 54 W., Logan County.

This is the only specimen from a known level in the Cedar Creek member that is complete enough for comparison with the four species recognized by Sinclair (1922). In the P4 of this specimen the valley between the crests is unblocked, but in the bottom of the valley there is an incipient ridge that may be an undeveloped mure. Only in extreme wear would this ridge have produced anything resembling a blocked valley, and even then it would not have resembled the type of blocked valley seen in *Hyracodon nebraskensis*. P<sup>3</sup> has the two transverse crests well developed, with the anterior one turning back toward the tip of the posterior crest. Here again the valley is blocked only by a low ridge which is not equal in development to the two crests. The valley of P2 is completely blocked. The stage of wear is similar to that seen in figure 2A of SINCLAIR, 1922. This specimen would fall into the H. nebraskensis group as defined by Sinclair, although the premolars may best be described as trending toward the H. leidyanus type of pattern.

Cope (1873a, p. 2) described Hyracodon arcidens from the Oligocene of northeastern Colorado. The type is apparently lost; Sinclair (1922, p. 68) judged that Cope's description did not apply to specimen AMNH No. 6309 which was labeled by Cope as the type and which was figured by Cope & MATTHEW (1915, pl. CII). MATTHEW (1901, p. 357), SINCLAIR (1922, p. 68), and H. E. WOOD (1927, p. 26) recognized this speices, but it was placed in synonymy with H. nebraskensis (Leidy) by Scott (1941, p. 842). In Sinclair's (1922, p. 67) succinct discussion of the status of the species of Hyracodon he states: "For systematic and stratigraphic purposes they may be conceived as species, although some might wish to term them subspecies." Lacking knowledge of intermediate stages and in the absence of the blending of the diagnostic characters, Sinclair concludes that "they are probably to be regarded as distinct species, on the basis of constant association of constant differences." the other hand, SINCLAIR also points out that the species might represent the stages in the progressive evolution of the hyracodont line - a chronocline. His comment that ancestor and descendant continued to exist contemporaneously for a time reflects the concept that animal populations are made up of representatives of the ancestral form, the norm or optimum group, and the progressive forms which will be the norm of the next stage. With large quarry populations such a condition might be demonstrated for Hyracodon. This type of successive populations could be accepted as a single species. Scott's (1941, p. 841) reasons for synonymizing H. arcidens, selenidens, leidyanus, and apertus with H. nebraskensis were: Stratigraphic separation is not possible; it is improbable that four species or subspecies lived "together" in South Dakota and Nebraska; and insufficient allowance has been made for the differences due to age and sex and to an uncommon degree of individual variability. Both SINCLAIR and Wood thought some stratigraphic division was possible. Scott's argument concerning species and subspecies was in the sense observed by neozoologists, but it would not necessarily apply to morphological units as used by Wood and would be untenable if stratigraphic division exists. Scott cited the variation seen in the specimens of Trigonias from the Trigonias Quarries in Weld County, Colorado, as an example of the degree of variation one might expect in Hyracodon, which is his best reason for synonymizing the five species. Specific designation for each group, if they are but morphological variants of a single species in the sense implied by Scott, does not seem desirable. On the other hand, the apparent trend toward formation of the separated and parallel crests in the premolars deserves recognition. So far as I am concerned, a single species with its several subspecies is probably the best means of showing the different stages in the

changing premolars, but this view yet remains to be adequately demonstrated.

#### Hyracodon sp.

Referred specimens.—Horsetail Creek member: No. 9004; fragments of lower molar; N½ sec. 31, T. 11 N., R. 56 W., Weld County. No. 9008; fragments of upper molar; SE½ sec. 1, T. 10 N., R. 54 W., Logan County. No. 9118; fragments of upper and lower teeth; W½ sec. 9, T. 10 N., R. 51 W. Logan County.

W., Logan County.

Vista member: No. 9051; right lower jaw and left maxillary with damaged teeth (not associated); SE% sec. 8, T. 11 N., R. 53 W., Logan County.

This material is too poor for specific identification, but it does not appear to differ from Hyracodon nebraskensis of the Cedar Creek member.

#### Family RHINOCEROTIDAE Owen, 1845

#### Trigonias osborni Lucas

Trigonias osborni Lucas, 1900, p. 221.

Referred specimens. — Horsetail Creek member: Univ. Colorado Mus. No. 18000; mandible with complete dentition; Trigonias Quarries, sec. 26 (Lower Quarry), and 27 (Upper Quarry), T. 10 N., R. 57 W., Weld County. No. 9006; left P<sub>3</sub>-M<sub>2</sub> in fragment of jaw; N½ sec. 31, T. 11 N., R. 56 W., Weld County. No. 9007; right M<sub>1</sub>-M<sub>2</sub>; SE½ sec. 1, T. 10 N., R. 54 W., Logan County.

The occurrence of Trigonias in the Chadronian of Weld County has been discussed by GREGORY & Cook (1928), Figgins (1934a), H. E. Wood (1931), MATTHEW (1930, p. 272; 1931, p. 5), and Scott (1941, p. 785). There is no reason to repeat in detail all the comments upon the specimens recovered from these quarries. In brief: Gregory & Cook (1928) reported two varieties of T. osborni Lucas and four new species, T. hypostylus, T. precopei, T. preoccidentalis, and T. taylori. MATTHEW (1930, 1931) considered only one genus and one species to be present. H. E. Woon (1931) recognized T. o. osborni, T. o. precopei (which included T. preoccidentalis), T. hypostylus, T. taylori, and described and named as new T. cooki. Figures (1934a) reduced all to one species, T. osborni. Scott (1941) considered two species to be present, T. osborni and T. taylori.

The specimen in the University of Colorado Museum has very large canines. The length of P1-M3 is 205 mm. (occlusal) and 220 mm. (alveolar) on

each side.

#### Caenopus premitis Gregory & Cook

Caenopus premitis GREGORY & COOK, 1928, p. 19.

Type.—Denver Mus. Nat. Hist. No. 1025 (skull E); Horsetail Creek member, White River formation, Trigonias Quarries, Weld County, Colorado.

This specimen has been discussed by Gregory & Cook (1928), Figgins (1934, 1934a), H. E. Wood (1931), and H. E. WOOD & A. E. WOOD (1937, p. On present evidence Caenopus premitis seems to be older than C. mitis.

# Caenopus mitis (COPE)

Aceratherium mite Cope, 1874a, p. 493. Caenopus mitis, Cope, 1880a, p. 611.

Type.—AMNH No. 6325; upper Titanotherium beds of Cedar Creek, Logan County, Colorado (fide Wood, H. E., 1927).

MATTHEW (1901, p. 357) first listed this species from the "Oreodon" beds, but later (1909, p. 104) listed the level as Chadron. The occurrence of Caenopus mitis in the Chadron of South Dakota lends weight to the view that the northeastern Colo-

rado specimens are Chadronian in age.

A specimen collected by H. T. MARTIN in 1911 from "Stone Ranch" (NW% of T. 11 N., R. 55 W., Logan County; locality data by oral communication from Curtis Hesse) might be referable to this genus. This specimen, No. 4917, a right lower jaw fragment, has a well-preserved second molar 30.5 mm. long and 17.5 mm. wide. Weak cingula are present on all sides except the internal surface. No cingula are visible on the exposed posterior or internal faces of the unerupted M<sub>3</sub>. The depth of the ramus at M<sub>2</sub> is 37.5 mm.

#### Subhyracodon occidentalis (LEIDY)

Rhinoceros occidentalis Ledy, 1851b, p. 276. Subhyracodon occidentale, Wood, H. E., 1927, p. 63.

Referred specimens.—Cedar Creek member (lower and middle): No. 174; an uncrushed and undistorted anterior part of a skull with complete dentition; ?eastern part of Weld County. No. 8213; mandible with damaged dentition; SE½ sec. 21, T. 11 N., R. 53 W., Logan County. No. 8363; anterior part of skull with right P²-M²; channel sandstones of sec. 9, T. 11 N., R. 55 W., Logan County.

This species was recorded from northeastern Colorado by Cope (1874a, p. 495) as "Several specimens from different localities." A second species from northeastern Colorado, Hyracodon quadriplicatus Cope (1873a, p. 1) [Aceratherium quadriplicatum (Cope) (1874a, p. 495) and Anchisodon quadriplicatus (Cope) (1879a, p. 270)] based on deciduous teeth, was considered indeterminable by H. E. Wood (1927, p. 68). Scott (1941, p. 810) made it a synonym of Subhyracodon occidentalis.

The University of Kansas specimens are unusual because of their large size. Both of the skull fragments have teeth the size of those in Subhyracodon metalophus, but the occlusal patterns are typical of S. occidentalis. The significance of this size and pattern combination must await better and more reliable evidence. This may be a case of increased size preceding pattern change in the evolution toward S. metalophus or it may merely record a local population of large S. occidentalis.

#### Rhinocerotid sp.

Referred specimens.—No. 8364; right maxillary with P<sup>2</sup>-M<sup>1</sup>; N½ sec. 13, T. 11 N., R. 56 W., Weld County. No. 8365; right M<sup>1</sup>-M<sup>2</sup>; SE¼ sec. 3, T. 11 N., R. 54 W., Logan County.

The Weld County specimen was found in graywhite silt at the base of a channel sandstone, and the other specimen was found 230 feet below the white marker in gray-white silt. Although each was below the main channels in the area, it is difficult to determine whether they were in the upper part of the Horsetail Creek member or lowermost part of the Cedar Creek member.

The teeth of both specimens are slightly smaller than those of *Subhyracodon occidentalis* found in the area and appear somewhat like the teeth of *Trigonias*. If it could be established that the teeth were those of *Trigonias*, this fact would be of considerable aid in determining the Chadronian-Orellan boundary.

# ORDER ARTIODACTYLA OWEN, 1848 FAMILY LEPTOCHOERIDAE MARSH, 1894

## Stibarus obtusilobus Cope

Stibarus obtusilobus Cope, 1873b, p. 3.

Type.—AMNH No. 6784; "Oreodon beds of northeastern Colorado" (fide MATTHEW, 1903, p. 219).

Referred specimens.—Horsetail Creek member: No. 8972; left P<sub>3</sub> in fragment of jaw; W% sec. 9, T. 10 N., R. 51 W., Logan County. No. 9105; left P<sub>2</sub>, M<sub>3</sub>; W% sec. 29, E% sec. 30, T. 11 N., R. 53 W., Logan County.

The specimens listed above have three large and distinct cusps on the trenchant premolars. The heel of  $M_{\rm s}$  is narrow and reduced. In size, the teeth are near those of *Leptochoerus spectabilis* and much larger than those of *Stibarus lemurinus*.

No. 8972 is directly comparable with Cope's type, which consists of a lone P<sub>s</sub> in a fragment of bone. Our material and the type (the only known specimens from northeastern Colorado) can be readily distinguished from the large leptochoerids found in the Cedar Creek member, which do not have trenchant and cuspate premolars or reduced third molars. Comment on the characters that distinguish Stibarus as a valid genus is made in the discussion of Stibarus lemurinus.

The occurrence of *Stibarus obtusilobus* in the Horsetail Creek member may explain its rarity, inasmuch as these beds are relatively barren of fossils.

## Stibarus Iemurinus (COPE)

Menotherium lemurinum Cope, 1873d, p. 419. Leptochoerus lemurinus, Matthew, 1899, p. 60. Leptochoerus spectabilis (in part), Scott, 1940, p. 368.

Type.—AMNH No. 5349; Oligocene of northeastern Colorado.

Referred specimens.—Horsetail Creek member: Uncatalogued Univ. Colorado Mus. specimen; left M<sub>1</sub>; W½ sec. 9, T. 10 N., R. 51 W., Logan County. No. 9225; right maxillary fragment with P<sup>2</sup>-M<sup>3</sup>; SW½ sec. 29, T. 11 N., R. 53 W., Logan County.

Cedar Creek member: Univ. Colorado Mus. No. 19863; right P<sub>4</sub>-M<sub>1</sub>; sec. 7, T. 11 N., R. 53 W., Logan County. No. 9033; right M<sub>1</sub>, and left M<sup>2</sup> (not associated); SW% sec. 12,

T. 11 N., R. 54 W., Logan County. No. 9230; left  $M_1$ - $M_2$ ; SE¼ sec. 31, T. 12 N., R. 54 W., Logan County. No. 9231; right  $M_1$ - $M_3$ ; locality same as No. 9033.

Matthew (1901, p. 357) reported the occurrence of Stibarus lemurinus in northeastern Colorado as Leptochoerus lemurinus. Scott (1940, p. 368) considered the type indeterminable and placed S. lemurinus in the synonymy of Leptochoerus spectabilis Leidy. However, with the series of northeastern Colorado specimens at hand, there is no difficulty in recognizing the species, either by comparison

with the type or with Cope's description.

The distinguishing features of the lower teeth of Stibarus lemurinus are: cusps higher than those in Leptochoerus spectabilis, S pattern of wear in the molars, narrow M<sub>s</sub>, and small size. The upper jaws listed above are referred to this species because of agreement in size. P2 is elongate and narrow, tri-cuspid, and much like the second premolar of Stibarus obtusilobus. P3 is about the same size as P<sup>2</sup> (Table 21) but has three external cusps and a fourth internal one which is small, semi-isolated, and opposite the central external cusp. P4 is molariform and equal to M1 in size. M3 is reduced. All the teeth are low crowned. This species is smaller than S. obtusilobus. Some supporting evidence for association of these upper and lower jaws is seen in Nos. PM476, PM477, PM481, and P25809 in the Chicago Natural History Museum, which are referable to this species. These Nebraskan specimens consist of upper and lower teeth collected from a single locality.

This species is placed in the genus *Stibarus* because of the narrow tricuspid condition of P<sup>2</sup> and the similarity of the lower molars of S. *lemurinus* 

to those of S. montanus.

Several features appear on the teeth of Stibarus

TABLE 21.-Measurements (in mm.) of Stibarus lemurinus

	No. 9225	No. 9231	No. 19863
Crown length of P2-M3	29.7		****
P2, antero-posterior length	7.2		
P2, transverse width	2.4		
P3, antero-posterior length	7.1	1777	1111
P3, transverse width	4.7	2.2.4.20	100000
P4, antero-posterior length	4.2	2002	1200
P4, transverse width	6.4	Nagar	4000
M <sup>1</sup> , antero-posterior length	4.6		
M1, transverse width	6.4		
M <sup>2</sup> , antero-posterior length	4.1	4.00	(7/5/5/5/ (#)#(#)#(
M <sup>2</sup> , transverse width	6.0	*****	3000000
M <sup>3</sup> , antero-posterior length	3.2	* * * * * * * *	* * * *
M <sup>3</sup> , transverse width	4.6		2444
P4, antero-posterior length	2022	22222	6.1
P4, transverse width	202222	12.37.47.6	3.4
M <sub>1</sub> , antero-posterior length	12.27.2.1	4.8	4.8
M <sub>1</sub> , transverse width	2222	8.7	3.7
M <sub>2</sub> , antero-posterior length		4.2	
M <sub>2</sub> , transverse width		3.6	
M <sub>3</sub> , antero-posterior length	2000	4.7	33315
M <sub>3</sub> , transverse width	3000 E	3.1	*****

a. University of Colorado Museum.

that are diagnostic for the genus. The upper and lower anterior premolars are cuspate and trenchant. The heel of M<sub>3</sub> is reduced. A distinct paraconid is present on the molars, although lost with wear.24 A character that may prove of value, if it can be demonstrated to be fairly constant, is the S pattern of wear in the lower molars. In Stibarus the S is formed by a crest that unites the hypoconid and metaconid, whereas in Leptochoerus the union is generally between the hypoconid and protoconid. The distinction is not great, and a little variation in Leptochoerus will result in the hypoconid uniting with the metaconid but no S pattern results from wear. Scott (1940, p. 372) indirectly referred to the S pattern when he described the lower molars of Stibarus: "The anterior half of the crown, consisting of two conical cusps, rises somewhat above the posterior half, suggesting the tuberculo-sectorial pattern; the posterior half is an obscurely-indicated crescent, which opens internally."

# Leptochoerus spectabilis LEIDY

Leptochoerus spectabilis Leidy, 1856, p. 88.

Referred specimens.—Cedar Creek member: No. 9226; left P<sup>2</sup>-M<sup>3</sup>; sec. 22, T. 11 N., R. 52 W., Logan County. No. 9228; left P<sub>3</sub>-M<sub>3</sub>; SW¼ sec 21, T. 11 N., R. 53 W., Logan County. Univ. Colorado Mus. No. 19855; left M<sup>1</sup>-M<sup>2</sup>; W½ sec. 7, T. 11 N., R. 53 W., Logan County.

Vista member: No. 9014; left M<sub>1</sub>-M<sub>3</sub>; NE% sec. 17, T.

11 N., R. 53 W., Logan County.

Unlisted from the Cedar Creek member are numerous fragments of upper and lower jaws containing from one to three teeth.

The specimens are referred to this genus and species because none differ greatly from comparative material of Leptochoerus spectabilis, and the third lower premolar does not resemble that of Stibarus obtusilobus. Matthew (1901, p. 357) reported finding Leptochoerus spectabilis in northeastern Colorado.

No. 9226 has a thin second premolar (Table 22) that is essentially a single cusp with the most minute anterior and posterior cuspules.

Table 22.—Measurements (in mm.) of Leptochoerus spectabilis

																		1	No. 9226
Crown length of P2-M3												_							35.3
P2, transverse width	100	eso Uni				-			er er	et G		о. 	о:- -	5/2					3.7
P <sup>2</sup> , transverse width	200	10//		î		en.			200		e e	20					172	u Au	8.3
transverse width		900	-	-	2	600		100	1123	4	0.0	9	C+1						7.3
P4, antero-posterior length	041	200				20			um Us		e.	27	•	* 86	 	35			5.6
P4, transverse width	160		37	90		D.	.00		85		Z	2	30	30	0	30	702		8.6
M <sup>1</sup> , antero-posterior length	1	10.						9								ľ		ŝ	5.0
M1 transverse width																			7.9
vi-, antero-posterior lengti																			4.5
																			7.3
M <sup>3</sup> , antero-posterior length	1	413				- 1		:: °		ď							1.5		3.9
M <sup>3</sup> , transverse width	T- (9)		×	or.	×	TO FO	0			å	e. R				24		 5		5.5

<sup>24.</sup> Leptochoerus shows no indication, even on unworn teeth, that the paraconids were so well developed.

#### FAMILY ENTELODONTIDAE LYDEKKER, 1883

#### Archaeotherium ramosus (COPE)

Elotherium ramosum Cope, 1874, p. 27.

Archaeotherium ramosus, Camp, Welles, & Green, 1949, p. 251.

Type.—AMNH No. G393; northeastern Colorado.

#### Archaeotherium potens (MARSH)

Amnodon potens Marsh, 1893, p. 410. Archaeotherium potens, Camp, Welles, & Green, 1949, p. 251.

Type.—Yale Univ., Peabody Mus. Nat. Hist. No. 12042; northeastern Colorado.

TROXELL (1920, p. 431) questionably referred the latter of these two species to the "upper Brule," and Scott (1940, pp. 440-441) gave the same general age assignment for both species. Matthew (1901, pp. 356-357) tentatively referred material from the Horsetail Creek and Cedar Creek members to Archaeotherium ramosus but did consider (1909, p. 106) a Whitneyan age a possibility. Inasmuch as neither species has been found outside of Colorado and, for that matter, no additional specimens of A. potens, it is difficult to judge exactly where the types may have been collected. Nevertheless, if the locality of Marsh's collecting in 1870 was in the Chalk Bluff area of Weld County, as I am inclined to think it was, then the type of A. potens probably is not from the upper Oligocene. Likewise, Cope's specimen probably came from Weld County, and therefore from Horsetail or Cedar Creek beds.

Additional evidence bearing on the problem is seen in a mandibular symphysis of the "Pelonaxtype" in our collection (No. 8289) which was collected by H. T. Martin, probably in 1925. This specimen has written upon it, apparently in Martin's handwriting, "Elotherium N.E. Colorado Miocene." The matrix is so much like that seen in channel sandstone in sec. 9, T. 11 N., R. 55 W., Logan County, assigned to beds of the Horsetail Creek member or lowest part of the Cedar Creek member, and so unlike any matrix seen in the Miocene, that this rather flimsy evidence is introduced for what it may be worth as indicative of a late Chadronian or early Orellan age for the subgenus.

#### Archaeotherium mortoni LEIDY

Archaeotherium mortoni Leidy, 1850, p. 90.

Referred specimens.—Horsetail Creek member: Denver Mus. Nat. Hist. collection of skeletons from Weld County. Cedar Creek member: No. 7728; skull and mandible; NE¼ sec. 3, T. 11 N., R. 54 W., Logan County.

This species is well known from the Chadronian beds of Weld County where the Denver Museum of Natural History has collected excellent specimens. Most of the fragmental material from the Horsetail and Cedar Creek members has been referred to Archaeotherium mortoni despite small differences in pattern and size of the teeth.

# Archaeotherium crassum (MARSH)

Elotherium crassum MARSH, 1873, p. 487. Archaeotherium crassum, TROXELL, 1920, p. 375.

Type.—Yale Univ., Peabody Mus. Nat. Hist. No. 12020; titanothere zone, northeastern Colorado.

The type of this species has been assigned, questionably, to beds of Orellan age (TROXELL, 1920, p. 375), but Marsh (1893, p. 408) mentioned associated titanothere bones. Matthew (1901, pp. 356-357) tentatively assigned material from beds of both Chadronian and Orellan age to this species. The only occurrence of Archaeotherium crassum outside of northeastern Colorado is a specimen, referred to this species by Clark (1937, p. 304), from the middle member of the Chadron of South Dakota.

# FAMILY TAYASSUIDAE PALMER, 1897

#### Perchoerus nr. P. minor Cook

Referred specimens.—Horsetail Creek member: No. 8237; fragment of jaw with P<sub>4</sub>-M<sub>1</sub>; N½ sec. 31, T. 11 N., R. 56 W.. Weld County. No. 9000; left M<sub>1</sub>-M<sub>2</sub>; W½ sec. 9, T. 10 N., R. 51 W., Logan County.

Heretofore this genus has been unknown from northeastern Colorado, and it is unfortunate that of the specimens collected none are satisfactory for reliable specific identification.

The two specimens from the Chadronian beds are referred to *Perchoerus minor* because of their small size (Table 23) and simple tooth pattern.

#### Perchoerus nr. P. nanus (MARSH)

Referred specimens.—Cedar Creek member (lower): No. 8236; fragment of maxillary with P<sup>4</sup>-M<sup>1</sup>; SW% sec. 21, T. 11 N., R. 53 W., Logan County.
Vista member: Univ. Colorado Mus. No. 19873; incom-

Vista member: Univ. Colorado Mus. No. 19873; incomplete left lower jaw containing P<sub>3</sub>-M<sub>3</sub>, and crushed right jaw with part of P<sub>1</sub>; SE¼ sec. 8, T. 11 N., R. 53 W., Logan County.

Assignment of these specimens to *Perchoerus* nanus is only in recognition of their small size. No. 8236 has teeth smaller than those in specimens of *P. probus* Leidy.

Typical of material from the Vista member, specimen No. 19873 has undergone distortion and damage during preservation. The incisors are crushed. The roots of the canines are present, and they indicate that these teeth were large and triangular in cross section. The first premolar is single rooted, and it is much closer to the canine than to the second premolar. The root of P<sub>2</sub> indicates that this tooth was smaller than P<sub>3</sub>. P<sub>3</sub> is exceptionally short and trenchant. It has a well-developed, postero-internal, basined heel. P<sub>4</sub> is partly molariform, with the metaconid almost as well developed as the protoconid. The paraconid is low and is united to the protoconid by a crest. The heel of P<sub>4</sub>, like that of P<sub>3</sub>, is the widest part of the tooth and is basined linguad of the hypoconid. M<sub>1</sub> is much worn and